THESIS

SAMPLING METHODOLOGY TRADEOFFS: EVALUATING MONITORING STRATEGIES FOR THE ENDANGERED HUMPBACK CHUB (*GILA CYPHA*) IN THE LITTLE COLORADO RIVER, ARIZONA

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ABSTRACT

SAMPLING METHODOLOGY TRADEOFFS: EVALUATING MONITORING STRATEGIES FOR THE ENDANGERED HUMPBACK CHUB (*GILA CYPHA*) IN THE LITTLE COLORADO RIVER, ARIZONA

Implementation of a reliable monitoring program is essential to informed population management. When recovering a sensitive species, priority should be on minimizing human induced negative effects, given already reduced population abundance. Thus, it is crucial to evaluate monitoring programs and make changes when more efficient techniques become available.

To assess tradeoffs in sampling effort first necessitates obtaining accurate demographic parameter estimates. However, obtaining such estimates may be challenging especially when assessing a migratory species monitored on its spawning ground. Due to concerns regarding sampling availability, in such cases, it may be necessary to evaluate temporary emigration from the study site to avoid generating biased estimates of survival, detection and spawning probabilities. Evaluating temporary emigration is especially important when non-annual spawning is anticipated, as skipped spawners may be unavailable for detection during annual sampling events.

Since the late 1980s, population monitoring for the potamodromous humpback chub (HBC) *Gila cypha* within the Lower Colorado River Basin (LCRB) has focused on hoop-net sampling within their primary spawning ground, the Little Colorado River (LCR). However, questions remain unanswered regarding their spawning strategy. Thus, due to the likely presence

of both resident and migratory fish and suspected non-annual spawning, I evaluated temporary emigration from the LCR, which I equate to skipped spawning. Using, robust design mark-recapture methodologies, I was able to generate unbiased estimates of survival and skipped spawning probabilities as well as spawner abundance.

Given concern for handling induced stress due to intensive hoop-net sampling and to gain additional insight into HBC life history strategies and population dynamics, in 2009, a passive detection system (i.e. full duplex PIT tag antenna array) was implemented in the LCR. With the addition of the array, this afforded an opportunity to evaluate sampling methodology tradeoffs between hoop-netting and array detections. Thus, using simulation analysis, and demographic parameter estimates generated from my skipped spawning analysis, I assessed the potential benefits and shortcomings of reducing hoop-net sampling effort and supplementing recapture data with passive array detections.

From my analysis, I found considerable evidence for skipped spawning among both male and female HBC. Females on average had a higher probability of failing to spawn in a year subsequent to spawning (i.e. $\hat{\gamma}''_{male}$ = 0.46 (95% credible interval [CRI]: 0.11, 0.81) and $\hat{\gamma}''_{female}$= 0.55 (95% CRI: 0.30, 0.75), although better sexing data is necessary to confirm this difference. Annual variability in skipped spawning probability was high (i.e. process variance (σ^2) = 0.306) while survival probability remained stable throughout the study period (i.e. $\hat{\bar{S}}$ = 0.75 (95% CRI: 0.66, 0.82), σ^2 = 0.005). Based on my most reliable skipped spawning probability estimates, (i.e. probability a spawner transitions to a skipped spawner ($\hat{\bar{\gamma}}''$) = 0.45 (95% CRI: 0.10, 0.80) and a skipped spawner remains a skipped spawner ($\hat{\bar{\gamma}}'$) = 0.60 (95% CRI: 0.26, 0.83)) which exclude sex, I found HBC in the LCRB have an average breeding cycle of every 2.12 years, conditional on survival.

By employing these estimates in simulation analysis, I found that hoop-net sampling can be reduced and supplemented with array detections without negatively affecting estimability of adult HBC survival and skipped spawning probabilities, given detection efficiency of the array remains sufficiently high. Because the array provides insight outside of traditional sampling periods and does not require repeated handling of this imperiled fish, it affords a viable means of reducing hoop-net sampling effort, thus, offering a potentially more efficient monitoring strategy.

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CHAPTER 1: HUMPBACK CHUB (*GILA CYPHA*) SPAWNING STRATEGY IN THE LITTLE COLORADO RIVER, ARIZONA

Introduction

The humpback chub (HBC) *Gila cypha*, originally described by R. R. Miller in 1945 (Miller 1946), is a long-lived cyprinid endemic to the Colorado River Basin (CRB; Holden and Minckley 1980). Its distribution within the CRB is patchy and primarily restricted to canyon-bound reaches characterized by deep-water and swift currents (Douglas and Marsh 1996). Although its historic abundance is not fully understood, it is surmised to currently occupy 68% of its historic range (Tyus 1998; USFWS 2011). Six populations have been identified, of which five occur in the Upper Colorado River Basin (UCRB) in the Yampa, Green and Colorado Rivers. The largest of the six populations occupies the Lower Colorado River Basin (LCRB), in which HBC primarily reside in the Colorado (CR) and Little Colorado Rivers (LCR; Douglas and Marsh 1996; USFWS 2002).

Due to its limited abundance, the HBC was included on the first list of endangered species published in the Federal Register in 1967 and has retained its endangered status since that time, with current protection afforded by the Endangered Species Act of 1973 (USOFR 1967; USFWS 2011). Primary threats impacting population persistence include: habitat loss due to flow modifications and water temperature reduction resulting from dam construction, as well as the introduction of non-native predatory and competing species (Marsh and Douglas 1997; Valdez and Ryel 1997; Clarkson and Childs 2000; USFWS 2002; Yard et al. 2011).

Although HBC in the LCRB were thought to originally spawn throughout the CR in Grand Canyon, in recent years, successful breeding and larval rearing has been predominantly

restricted to the lower 14.2 km of its largest tributary, the LCR (Valdez and Ryel 1995; Robinson et al. 1998; Gorman and Stone 1999). Hypolimnetic releases from Glen Canyon Dam have been implicated in reducing available breeding habitat within the LCRB (Valdez and Ryel 1995; Kaeding and Zimmerman 1983; Douglas and Marsh 1996; USFWS 2002). Since dam construction, year-round water temperatures in the CR downstream of Lees Ferry typically range from 8 to 12°C as compared to pre-dam summer temperatures ranging between 25 to 30°C (Wright et al. 2009). The unregulated LCR provides annual high water temperatures similar to pre-dam conditions found within the CR (Van Haverbeke et al. 2013). Despite temperature limitations in the CR, observations have been made of larval HBC in warm springs within the CR, indicating small scale spawning may occur. However, evidence is sparse for recruitment success beyond the LCR (Valdez and Masslich 1999; Andersen et al. 2010).

Unlike many large river potamodromous fishes, undergoing long distance migrations to complete their life cycles, HBC movement within the LCRB has been largely restricted to the lower 14.75 km of the LCR and a 20 km section of the CR centered on the LCR confluence (Valdez and Ryel 1995; Paukert et al. 2006). Limited numbers of HBC have exhibited longer distance migrations; however, in all documented cases, movement occurred between the CR and the LCR. Regardless of distance migrated, HBC demonstrate strong site fidelity even over extended periods of time. Consequently, the LCR provides an ideal location for monitoring abundance trends for the entire LCRB population of HBC (Paukert et al. 2006).

Traditional sampling and population estimation techniques for the LCRB population of HBC have focused on tracking changes in abundance and recruitment within the LCR through mark-recapture methodologies. Since 2000, the U.S. Fish and Wildlife Service (USFWS) has employed a Chapman modified Petersen closed population estimator (Seber 1982) to estimate

seasonal abundance (Van Haverbeke et al. 2013). In more recent years, an age structured open population model was developed to evaluate age specific annual mortality probabilities as well as abundance and recruitment trends (Coggins et al. 2006). One primary assumption of these estimation techniques is that HBC spawn annually, and are, therefore, available for detection during LCR sampling events. However, questions remain unanswered regarding whether a portion of the adult population fails to enter the LCR annually as a result of skipped spawning. Due to uncertainty regarding sampling availability, annual spawning migrations present challenges when estimating demographic parameters.

While iteroparous fishes, such as HBC, have traditionally been considered annual breeders, more recent research supports the idea that not all fishes spawn with annual regularity (Rideout and Tomkeiwicz 2011). Life-history theory suggests skipping reproductive events may have evolved as a mechanism to maximize lifetime fitness, especially in response to poor environmental conditions (Jørgensen et al. 2006). Most commonly, fisheries research has attributed skipped spawning to density-dependent effects resulting from dietary deficiencies (Rideout and Tomkeiwicz 2011; Skjæraasen et al. 2012). A recent study presents unequivocal evidence for high rates of skipped spawning among female Northeast Arctic cod. In this population, individuals that skipped spawning were estimated to be equally abundant as spawners and principally remained on feeding grounds while spawners migrated southward to breeding habitats (Skjæraasen et al. 2012). Although the majority of fisheries research regarding skipped spawning has focused on females, limited evidence of skipped spawning has also been documented in males with spawning probability as low as 0.75 (Rideout and Tomkiewicz 2011). Such research motivates the importance of evaluating skipped spawning, especially when resources are thought to be limiting. Understanding annual spawning probabilities in migratory

populations is especially important when sampling occurs on breeding grounds because skipped spawners would be unavailable for detection.

In the LCRB, additional challenges arise when evaluating HBC demographic parameters, particularly skipped spawning, due to the presence of both resident and migratory individuals (Douglas and Marsh 1996; Gorman and Stone 1999). Resident HBC are believed to inhabit the LCR year-round, while migratory adults primarily reside in the CR and enter the LCR to spawn. This form of life history heterogeneity, in which residents and migrants breed sympatrically but overwinter in different habitats, is known as 'non-breeding partial migration' (Chapman et al. 2011). Accounting for such differences in life history strategies is difficult, given uncertainty regarding the age or size at which individuals begin displaying migratory behavior. Research by Gorman and Stone (1999) suggests once a HBC reaches 300 mm total length (TL), migratory behavior appears obligatory and residency transitions from the LCR to the CR. However, Douglas and Marsh (1996) conclude two distinct populations exist: one that resides year-round in the LCR and a second that migrates between the two rivers for spawning purposes, regardless of age or size. If a portion of the LCRB population fails to spawn annually and instead resides year-round in the CR, they would be unavailable for detection during annual LCR monitoring events. If unavailability is not accounted for, demographic parameter estimates, such as survival and spawning probability, may be biased (Kendall and Nichols 1995; Kendall et al. 1997).

Thus, to increase understanding of HBC demographic parameters and minimize uncertainty regarding sampling availability, I evaluated long-term mark-recapture data from the LCRB using closed robust design mark-recapture models (Kendall et al. 1997). I generated estimates of annual skipped spawning, survival and detection probabilities, as well as spawner abundance, while incorporating multiple datasets to account for potential differences in

demographic parameters based on sex and migratory status. The primary focus of my research was to determine if, and at what probability, HBC in the LCRB fail to spawn annually, as this would have important implications for estimating abundance and survival probabilities used to evaluate population status and trends.

Methods

Little Colorado River Sampling

The USFWS, in cooperation with the U.S. Geological Survey, Grand Canyon Monitoring and Research Center (GCMRC), has been largely responsible for collecting HBC monitoring data in the LCRB. Since fall of 2000, they have consistently conducted four annual stratified hoop-net surveys in the lower 13.57 km of the LCR. Two surveys occur in the spring, typically in April and May, during the HBC spawning season, followed by two fall surveys in September and October. To conduct surveys, the lower 13.57 km of the LCR has been divided into three primary reaches and each primary reach has been subdivided into three secondary reaches (Figure 1.1). Three crews, generally consisting of 3 – 4 individuals are deployed to each primary reach for simultaneous sampling. Sampling typically takes place for three consecutive nights per secondary reach in which twenty hoop-nets (0.5 – 0.6 m diameter, 1.0 m long, single throat, 3 – 4 hoops, and covered with 6 mm mesh) are set in locations expected to yield catches of HBC. Hoop-nets are moved between nights within a secondary reach if catches are negligible or when alternative sites are available. Each crew fishes hoop-nets for nine consecutive nights, yielding a total of 540 net nights of sampling effort per survey (Van Haverbeke et al. 2013).

Upon capture, HBC $\geq$ 150 mm TL and at times down to 100 mm TL are uniquely marked with a passive integrated transponder (PIT) tag (Biomark Inc., Boise, ID; Persons et al. 2013).

Length, sex, reproductive status, external parasite data, and location of capture are all recorded prior to release (Van Haverbeke et al. 2013).

Additional HBC surveys in the LCR have been conducted by the Arizona Game and Fish Department (AGFD) since 1987. Sampling effort concentrated on the lower 1.2 km of the LCR consists of fishing 13 hoop-nets (1.0 m diameter, 5.0 m long, two throats, 7 hoops, and covered with 6.3 mm mesh) placed in standardized locations for 20 – 30 consecutive nights during April and May (Persons et al. 2009). Tagging protocols and data collected are consistent with those of the USFWS (Persons et al. 2013).

In May of 2009, a full duplex PIT tag antenna array (Biomark Inc., Boise, ID) was installed in the LCR by the GCMRC 1.78 km upstream of the confluence with the CR, to passively detect the passage of HBC moving into and out of the LCR (Figure 1.1). However, functionality has been variable primarily due to damage caused by annual high flow events, with additional limitations in early years caused by insufficient power to the array as a result of reduced sun exposure to the solar charging panels in winter months (W. Persons, U. S. Geological Survey, Grand Canyon Monitoring and Research Center, pers. comm.). In recent years, the array has been operational year-round.

Robust Design Closed Population Models

Using the USFWS long-term monitoring data along with GCMRC array detections, I estimated annual survival (*S*), detection (p), recapture (c), and skipping probabilities (γ) for adult HBC along with spawner abundance (N^s). I defined an adult as any HBC greater than or equal to 200 mm TL, which was based on research indicating reproductive maturity is typically reached after three years of age and a minimum TL of 200 mm (Valdez and Ryel 1995; Gorman and Stone 1999; Meretsky et al. 2000; USFWS 2002). To conduct my analysis, I employed

closed robust design mark-recapture models (Kendall et al. 1997) in program MARK (White and Burnham 1999). Because the USFWS's sampling protocols include repeated hoop-net sampling over short time intervals within a sampling "season" (i.e. a given survey), this provided an ideal opportunity to evaluate temporary emigration from the LCR through the use of Pollock's robust design (Pollock 1982). Under this model, within-season sampling periods are defined as secondary sampling occasions and are generally completed over consecutive days such that population closure can be assumed. Longer periods of time typically occur between primary sampling occasions (i.e. annual events) in which the population is assumed to be open. Between annual sampling events, HBC can remain in the LCR (if resident), return to the LCR, temporarily emigrate to the CR or die. One of the benefits of implementing this robust design model is the ability to separate availability (i.e. HBC that are in the LCR during sampling events) from true detection probability given presence in the study area (p^* = the probability of being detected at least once during a primary sampling occasion given presence in the study area). I assumed absence from the LCR during the spawning season is reflective of a failure to spawn, and I equate temporary emigration from the LCR with skipped spawning. Thus, I analyzed available hoop-net and array data from the LCR to evaluate evidence for skipped spawning in light of uncertainty regarding migratory status. I completed this modeling analysis by subdividing the data into three subsets to assess the importance of accounting for residency and sex specific parameterization.

Additional assumptions specific to the closed robust design mark-recapture model I implemented include: within season demographic (see Figure 1.2) and geographic closure (but see Kendall 1999), no tag loss or handling mortality, all marked animals must be identifiable as such and recorded correctly, all individuals grouped together (i.e. age, sex etc.) have the same

probability of capture, survival and emigrating, survival of the unobservable state is equal to the observable state, and each animal acts independently with respect to survival, movement and detection.

Data Sub-setting

To evaluate evidence for skipped spawning and facilitate unbiased parameter estimation, I first distinguished individuals appearing to display a migratory life history strategy from those that may be residing solely in the LCR. Based on the assumption resident adults live year-round in the LCR regardless of spawning status, they would presumably be available for detection year-round. However, because migratory HBC are assumed to only enter the LCR when reproductive, if HBC do not spawn annually, skipped spawning individuals would be unavailable for detection during LCR sampling events. Therefore, I selected only known migratory adults to evaluate skipped spawning. Although inclusion of residents would provide confidence for estimating survival probability, skipped spawning probability could be biased when equating availability with spawning probability.

My designation of a migratory spawner was any adult HBC captured in the lower reach of the LCR downstream of the PIT tag antenna array with initial release occurring above the array. I used all available data from the LCR to distinguish these individuals, which included USFWS and AGFD hoop-net captures, as well as GCMRC array detections. I incorporated AGFD detections solely to aid in designation of migratory individuals, given sampling was restricted to the lower 1.2 km of the LCR. I chose this approach because it likely provides a conservative estimate of migratory behavior, and I refer to this dataset as 'known migrant'. My strategy for defining 'known migrant' individuals was motivated by research from Gorman and Stone (1999) indicating a higher proportion of individuals captured in the lower reach of the

LCR (i.e. 0.0 – 3.0 km) were also captured in the confluence (i.e. CR) as compared to those captured in the upper reach (i.e. 10.5 – 13.57 km). Their findings are suggestive of a higher proportion of non-migratory HBC residing in the upper reach of the LCR. Additional support for my reasoning comes from research by Van Haverbeke et al. (2013), in which they found the majority of spawning and overwintering HBC occupy the upper reaches of the LCR (i.e. 5.0 – 13.6 km), indicating there is likely better spawning and overwintering habitat in this section of the river.

For comparison purposes, and to increase sample size due to the restrictive nature of the 'known migrant' data sub-setting, I relaxed my migratory assumption and instead assumed all adults were migratory. I refer to this larger dataset as 'all adults'. By making this assumption, I was able to use all HBC detections for reproductively mature adults from the USFWS long-term monitoring dataset along with array detections. Using all adult HBC detections greatly increased sample size (Table 1.1), as well as my ability to evaluate annual variability, and to more thoroughly evaluate skipped spawning and assess sex specific differences in demographic parameters. Using all adult HBC detections also allowed me to evaluate the importance of accounting for residency when evaluating skipped spawning. If a large portion of the population consisted of resident adults, I expected skipped spawning probability would be reduced under the 'all adults' dataset because resident individuals would be present in the LCR regardless of spawning status. However, when comparing skipped spawning probability estimates between the 'known migrant' and 'all adults' datasets, if I did not see a negative bias in skipped spawning probability when including all adults, accounting for residency may not be necessary when assessing skipped spawning.

Given concern regarding potential sex specific differences in annual skipped spawning, survival and detection probabilities, I also analyzed the 'all adults' dataset while accounting for sex. To do so, I restricted the data to detections of ripe individuals due to challenges in sexing individuals when gametes are not expressible. As a result, sample size was significantly reduced from the 'all adults' dataset (Table 1.1). Interestingly, the resulting dataset was also heavily male biased (i.e. 95% males). Finding a high proportion of ripe males did not indicate the population was male biased, but suggested males may have been expressing gametes for a longer period of time or their gametes were easier to detect. I refer to this dataset as 'known sex'.

Sampling Occasions

Because my primary focus was to evaluate skipped spawning, I only included spring sampling occasions (i.e. April and May) and detections of adult HBC. Using a robust design framework, I designated the first day of USFWS hoop-net sampling at a given location as the first of three secondary sampling occasions. I then pooled the subsequent 2 days of sampling at a given location into a single detection event, yielding my second secondary sampling occasion (Figure 1.2). I repeated this process for both April and May sampling occasions and combined the datasets by pooling the first days of sampling into the first detection period and all subsequent days of sampling into the second detection period. Pooling was done to mitigate the possible effect of closure violation. My third secondary sampling occasion consisted of all spring PIT tag antenna array detections from May. An example within season capture history of 101, where "1" indicates capture and "0" no capture, would denote an individual was captured on day 1 of USFWS hoop-net sampling at a given location, was not recaptured on days 2 or 3 of hoop-net sampling but was detected by the array. Ideally, I would have also pooled array detections across March and April to include any fish crossing the array earlier in the season as

they migrate upstream to spawn. However, during the years for which I had available data, the array was not operational during March and April and in some years was only operational for a portion of May.

Although consistent hoop-net sampling by the USFWS began in 2001, detections from 2001 to 2003 were not included in the 'known migrant' dataset due to the number of sampling periods necessary to designate a migratory individual. However, due to elimination of the migratory assumption, the 'all adults' and 'known sex' datasets include detections from 2001 to 2011. Array detections were only available from 2009 to 2011, resulting from its recent installation. Therefore, the third secondary sampling occasion was only available for the last three years of the study. Additionally, initial release of individuals was based on hoop-net data alone because a fish must be captured before being released, and array detections are not valid for this purpose.

Modeling Analysis

When evaluating evidence for skipped spawning, I tested three hypotheses regarding the process driving this behavior. I began by modeling spawning as a function of reproductive status in the previous year and define this as a first-order Markov process. Under this hypothesis, the mechanism responsible for a HBC skipping a spawning event in a subsequent year is biological, indicating a need to build up resources prior to spawning. Markovian breeding processes have been documented in various species, including sea turtles, amphibians and birds (Kendall and Bjorkland 2001; Rivalan et al. 2005; Barbraud and Weimerskirch 2012; Prince and Chaloupka 2012). In a robust design framework, I tested my Markovian hypothesis by allowing transition from an observable state (i.e. spawner) at time (t) to an unobservable state (i.e. skipped spawner) at time (t+1) (i.e. $\gamma_t^{''}$) to differ from remaining in an unobservable state (i.e. skipped spawning

state ($\gamma_t^{'}$)). My second hypothesis predicted spawning was a completely random process in which environmental factors were driving reproductive ability due to fluxes in resource availability. Under a random spawning process, the probability of spawning at time (t+1) is independent of spawning status at time (t), indicating current environmental conditions dominate the decision to spawn. I tested this hypothesis by setting the transition probability of a spawner becoming a skipped spawner ($\gamma^{''}$) equal to the probability of a skipped spawner remaining a skipped spawner ($\gamma^{'}$). My third hypothesis predicted all reproductively mature HBC in the LCRB spawn annually. To model this hypothesis, I set $\gamma^{''}$ equal to zero, indicating no transitions were taking place, and I refer to this as a no skipped spawning model. I allowed the Markovian and completely random skipped spawning models to vary over time or remain constant.

To thoroughly evaluate demographic parameters, I also allowed survival probability estimates to vary over time or remain constant, given constraints. Because HBC detections were limited to the LCR, this required assuming survival of unobservable individuals (i.e. skipped spawners) equals survival of observable individuals (i.e. spawners). However, current understanding is limited regarding potential similarities or differences in river specific (i.e. CR or LCR) or reproductive status (i.e. spawners or skipped spawners) specific survival probabilities. Although, a concurrent LCRB study, found that during a period of consistently warmer water temperatures in the CR, HBC survival was higher in the CR than in the LCR (Yackulic et al. 2014). Additionally, terminal time-specific skipped spawning probability estimates (i.e. $\gamma_k^{''}$and $\gamma_k^{'}$) are confounded with terminal time specific survival estimates under a Markovian emigration process (Kendall et al. 1997, Schaub et al. 2004). To account for this parameter inestimability required constraining $\gamma_k^{''}$ and $\gamma_k^{'}$. Therefore, to evaluate annual variation in survival probability

while accounting for this limitation, I set $\gamma''_{k-1} = \gamma''_k$ and $\gamma'_{k-1} = \gamma'_k$. I selected this constraint *a priori*, because they were likely the most similar.

I also accounted for differences in detection probability based on time and trap response. I evaluated trap response by allowing initial within season capture probability (p) to differ from within season recapture probability (c) with no annual variation or trap response across years. I refer to this as model $p(.)$, $c(.)$, indicating a behavioral effect only. I created a second behavior model, this time allowing for annual and within season variability, and I refer to this as model $p(t,j)$, $c(t)$. Because the final capture and recapture probabilities both reflect array detections, I set these values equal, thus allowing for within season variation in p during the years in which array detections were available. However, when array detections were not available, fully time varying, within season detection probabilities were not estimable in conjunction with a trap response. Thus, I set $p(t,1) = p(t,2)$. I then created a time varying model excluding a behavior effect which allowed for full time variation in p, both within and among years, and I refer to this as model $p(t,j)$. I also created a time varying model with only annual variability, again constraining $p(t,1) = p(t,2)$, and I refer to this as model $p(t)$. My final detection probability model was both time constant and excluded a behavior effect. I considered this a null model, and I refer to it as model $p(.)$. Additionally, I did not allow for a trap response based on array detections because this is a passive detection process and unlikely to elicit a response based on previous detection.

The closed robust design model I employed, based on work by Otis et al. (1978) and Kendall et al. (1995), includes within season abundance estimates (N_t) in the likelihood, thus providing a reasonable method for estimating LCR spawner abundance (N^s). From my abundance estimates, I was able to make comparisons between my estimation methods and the

traditional Chapman modified Petersen closed population estimation techniques implemented by the USFWS. To employ the standard closed robust design abundance estimator, I assumed the entire spawning population was available for detection (i.e. there were no places in the LCR where spawning HBC were not being sampled), and the timing of sampling corresponded with their spawning season (i.e. spawners were not migrating in and out of the LCR between sampling events). In all models, spawner abundance was time varying (N_t^s).

I then created all possible combinations of the parameters of interest for a total of 60 models. All of which are reasonable in this light. To evaluate sex specific parameterization, I allowed all parameter estimates to vary between males and females and compared those to sex constant models for a total of 120 models. A full list of models and estimable parameters is available in the Appendix.

In program MARK, for each model, parameters were estimated using a sin link. However, when generating the most reliable parameter estimates, I implemented a Markov Chain Monte Carlo (MCMC) parameter estimation procedure using a logit link because the logit link is a monotonic transformation and is less prone to errors than the sin link. I report MCMC estimates because this method provides 95% credible intervals (CRI) which may perform better than a 'frequentist' (i.e. profile likelihood-based 95% confidence intervals [CI]) approach when estimability issues near the 0 – 1 bounds arise (Cooch and White 2013). From the MCMC analysis, I was able to estimate a grand mean (μ) and process variance (σ^2), given sufficient time-varying estimates, for *S* and γ using a random effects model. To generate MCMC parameter estimates, I used 4000 "tuning" samples, 1000 "burn in" samples and stored enough samples to yield convergent iteration plots (i.e. 'known migrant' = 200,000, 'all adults' = 50,000, 'known

sex' = 100,000). I used a default prior mean of 0 and standard deviation of 1.75 for beta parameters not included in random effects.

Model Selection

For each dataset, model selection was based on information theory, while initial parameter estimates were based on a maximum likelihood approach. I determined model support using Akaike Information Criteria with a small-population correction factor (i.e. AICc), and I refined parameter estimates from my most parsimonious models using MCMC. I determined the theoretical number of estimable parameters, and adjusted AICc values from MARK to account for any discrepancies due to parameter inestimability as a result of data limitations. Additionally, any model displaying convergence issues was eliminated from the analysis. Attempts were made using alternative optimization techniques and providing starting values to remedy convergence issues; however, in most cases attempts were unsuccessful. When reporting top models, I included all models with $\Delta AICc \leq 7$. Analysis by Burnham et al. (2011), indicates strong support for models with $\Delta AICc \leq 2$; however, they emphasize this should not be used as an arbitrary cutoff. Additional support can be found for models in the $\Delta AICc$ 2 – 7 range and should not be dismissed.

Because model selection approaches rely on the most general model adequately fitting the data (Burnham and Anderson 1998), I used the median $\hat{c}$ procedure in program MARK to evaluate goodness of fit (Cooch and White 2013). Although this method cannot be directly applied to a robust design model, using a multistate framework, I created a model with an unobservable state (i.e. skipped spawners), which allowed me to employ the median $\hat{c}$ procedure. Thus, I was able to partially test the assumptions underlying my models by evaluating the amount of overdispersion in the data.

Results

I found overwhelming support for skipped spawning as indicated by all top models (i.e. AICc ≤ 7.0) including a skipped spawning process, with no support for consistent annual reproduction (Table 1.2). When accounting for a resident adult population, my most parsimonious model indicated skipped spawning was a completely random process, with time-constant *S* and γ, and annual variability in detection probability. Under this model, I saw evidence for a negative trap response based on average p and c estimates of 0.47 and 0.20, respectively. Although, my most parsimonious model revealed a completely random skipped spawning process, considerable model selection uncertainty was apparent based on total model weight (i.e. w_{random} = 0.60 and $w_{Markovian}$ = 0.40). When analyzing the 'all adults' dataset, I found reduced model selection uncertainty and strong support for a Markovian skipped spawning process. I also saw a shift to annually varying *S*, γ'' and γ', likely due to increased sample size. When accounting for sex, my most parsimonious model also provided support for a Markovian skipped spawning process and time-varying γ'', $\gamma'$and *p*. However, estimates of *S* were time-constant. Additionally, substantial support for sex-specific parameterization was indicated by all top models including unique parameter estimates for males and females. Although a trap response was indicated in the 'known migrant' analysis, no support was found for a trap response in either the 'all adults' or 'known sex' analyses.

Skipped Spawning Probability

When estimating skipped spawning probability, I evaluated all three datasets to assess the importance of accounting for residency and sex specific parameterization. First, I compared estimates from the most parsimonious model under my 'known migrant' dataset to the same model under my 'all adults' dataset. My time constant estimate of γ when evaluating only

'known migrants' was 0.65 (95% CRI: 0.57, 0.73) as compared to 0.69 (95% CRI: 0.66, 0.71) when including 'all adults'. The observed difference in γ was opposite in direction from my expectation if a large proportion of this population were resident adults. Additionally, to avoid any potential bias that may be generated because resident individuals are unlikely to be detected by the array, I then excluded array detections from the analysis and found γ was equal across datasets (i.e. γ('known migrant') = 0.49 (95% CRI: 0.29, 0.64), γ('all adults') = 0.49 (95% CRI: 0.45, 0.53) . Therefore, I concluded, accounting for residency may not be necessary when evaluating skipped spawning. By incorporating all adult detections this provided larger sample size and in turn greater power to evaluate annual variability in demographic parameters. Because my conclusions regarding skipped spawning were not influenced by residency and my 'known sex' dataset was heavily male biased, my most reliable demographic estimates come from my analysis of the 'all adults' dataset.

Since a Markovian skipped spawning process was strongly supported by the 'all adults' and 'known sex' datasets and some support was found under the 'known migrant' dataset, I estimated differences in future skipped spawning probabilities based on current spawning state. The average probability of an adult HBC skipping a spawning event in a year subsequent to spawning ($\hat{\bar{\gamma}}''$) was 0.45 (95% CRI: 0.10, 0.80), and the average probability of remaining a skipped spawner ($\hat{\bar{\gamma}}'$) was 0.60 (95% CRI: 0.26, 0.83), which translates to an expected 2.12 years between spawning events, conditional on survival. Annual variability in γ'' was high (i.e. σ^2 = 0.306), indicating the probability of a spawner transitioning to a skipped spawner was highly dynamic over the study period (Figure 1.3). However, annual variability in γ' was reasonably low (i.e. σ^2 = 0.085). After accounting for sex, I found females appear to have a higher probability of skipped spawning in a year subsequent to spawning than males based on $\hat{\bar{\gamma}}''_m$ = 0.46

(95% CRI: 0.11, 0.81) and $\hat{\bar{\gamma}}_f^{''}$ = 0.55 (95% CRI: 0.30, 0.75), although estimates reveal considerable sampling variability (Figure 1.4). I also found high process variance for $\gamma_m^{''}$, indicating the probability of a male transitioning from a spawner at time (t) to a skipped spawner at time (t+1) was highly dynamic. I found, on average, males have a higher probability of remaining a skipped spawner (i.e. $\hat{\bar{\gamma}}_m'$ = 0.60 (95% CRI: 0.26, 0.90)) than transitioning from a spawner to a skipped spawner. I present annually varying estimates for the probability of a female remaining a skipped spawner in a subsequent time period (i.e. γ_f'); however, I was unable to generate a reliable mean and process variance estimate due to data limitations. Although males and females, on average, appear to skip spawning with differing probabilities, better sexing data is necessary to confidently determine sex specific estimates.

Survival Probability

Annual adult survival probability estimates were reasonably consistent across datasets (Table 1.3) and over time (Figure 1.3). Under the 'known migrant' analysis, my most reliable estimate for annual adult survival probability was a constant 0.79 (95% CRI: 0.70, 0.88) over the study period (i.e. 2004 – 2011). I found annual survival probability did not differ significantly between males and females, with an estimated constant survival probability of 0.78 (95% CRI: 0.73, 0.83) for males and 0.76 (95% CRI: 0.63, 0.90) for females. When I included 'all adults' in the analysis, survival probability was annually variable. although the majority of annual variability was attributable to sampling variance (Figure 1.3). However, I did see a decrease in *S* in 2006, with an estimated probability of 0.57 (95% CRI: 0.48, 0.68), which warrants further exploration as to the mechanism. Survival probability was also reduced for the terminal two years of the study (i.e. 2009 and 2010), which may be attributable to modeling constraints (Langtimm 2009). Thus, I reran my MCMC random effects model excluding 2009 and 2010

estimates and found identical results (i.e. 0.75 (95% CRI: 0.68, 0.83)) as compared to when including all time intervals (0.75 (95% CRI: 0.66, 0.82)). Based on the grand mean estimate from my MCMC random effects model, I believe my most reliable estimate of annual adult survival probability is 0.75 as generated from my 'all adults' analysis.

Spawner Abundance

My estimates of spawner abundance (N_t^s, where s = current year spawning adult) show a fairly stable trend from 2001 until 2006 with an average of 1027 (Range: 835 to 1342) spawners, excluding 2002, when I estimated N^s to be 56 (95% CRI: 53, 70; Figure 1.5). Beginning in 2007 and continuing until 2010, I show a steady increase in spawner abundance up to a high of 3950 (95% CRI: 3427, 4574), with a slight decline in 2011. Because my 2002 estimate is considerably lower than all other estimates during the study period, this reduction is likely attributable to changes in sampling effort and not truly reflective of spawner abundance for that year.

Detection Probability

Time varying capture probability estimates indicated detectability via hoop-net sampling was dynamic over the study period (Figure 1.6), with an average day 1 detection probability estimate of 0.19 and a pooled day 2 and 3 estimate of 0.30. Array detection probability estimates were consistently low, as was expected, because the array was only operational for a portion of the HBC migratory period. On average, I estimated array detection probability was 0.03, ranging from 0.01 in 2009 and 2010 to 0.06 in 2011. Pooled detections across all gear types and within season sampling periods (i.e. p constant) showed low sampling variation but high annual variation, with detection probability estimates ranging from 0.07 to 0.24 and mean of 0.18.

Goodness of Fit

Median $\hat{c}$ estimates from the 'known migrant' and 'all adults' datasets indicate minimal overdispersion in the data, given median $\hat{c}$ of 1.187 (95% CI: 1.163, 1.210) and 1.177 (95% CI: 1.157, 1,197), respectively. Due to data limitations for the 'known migrant' dataset, my median $\hat{c}$ estimate was based on the most parsimonious model. However, given larger sample size, I was able to apply the median $\hat{c}$ procedure to my most general model for the 'all adults' dataset, barring one exception. The multistate model used to evaluate goodness of fit does not account for differences in trap response; therefore, my most general model did not include this parameterization. Because all median $\hat{c}$ estimates were sufficiently close to 1, indicating good fit of the model to the data, I did not adjust model selection values.

Discussion

Regardless of migratory status assumptions, my evidence strongly suggests adult HBC are skipping spawning events and as a result are not annually available for detection within the LCR. Although I do not formally evaluate spawning probability based on assessment of physical ripeness, given HBC in the LCRB are migratory and sampling was conducted on their spawning ground, I believe temporary emigration is an appropriate measure of skipped spawning. Due to strong site fidelity and limitations in suitable breeding habitat outside the LCR, research indicates HBC are unlikely to spawn in locations outside of the LCR (Ryel and Valdez 1995; Robinson et al. 1998; Gorman and Stone 1999; Paukert et al. 2006). If migratory adults enter the LCR during the breeding season for purposes other than spawning, which at this point has not been evaluated, my migratory status assumption would lead to negatively biased skipped spawning probabilities. However, given spawning omission is likely attributable to maximizing long-term fitness through increased survival and greater future spawning success

due to energy savings (Rideout et al. 2005); it is improbable adult HBC expend energy to migrate when non-reproductive.

When accounting for the possibility of a resident population within the LCR, I found nearly identical skipped spawning probability estimates as when including all adults, indicating either most adult HBC are migratory or my method for distinguishing migrants is invalid. Without further monitoring of movement patterns within this population or greater detections of HBC in the CR, inferences regarding residency of HBC in the LCR remain limited. However, support for a small resident LCR population comes from recently published research by Yackulic et al. (2014) in which they estimated 82% of adult HBC in the LCRB are migratory. Similar findings were reported by Limburg et al. (2013) based on otolith microchemistry in which they found 18% residency. However, all resident individuals were juveniles, while all adults migrated to the CR.

Although the spawning decision is apparently dependent on spawning status in the previous year, I can reasonably conclude, on average, a minimum of 50% of the adult population fails to spawn annually based on pooled estimates of γ'' and γ'. Similar findings are reported by a concurrent study revealing skipped spawning probabilities of 0.69 and 0.39, respectively for small (i.e. 200-250 mm TL) and large (i.e. 250+ mm TL) adults (reported as spawning probabilities (i.e. 1- skipped spawning probability; Yackulic et al. 2014)). When I evaluated my 'all adults' and 'known sex' datasets as compared to my 'known migrant' dataset, I found skipped spawning is best represented with a Markov process. It is not surprising, analysis of my 'known migrant' dataset indicated a completely random skipped spawning process because often with small datasets there is insufficient power to detect more complex effects. However, due to the likely presence of both resident and migratory HBC in the LCRB, an alternative hypothesis

for a completely random process appearing Markovian when incorporating all adult detections is inclusion of resident individuals. If both resident and migratory adults are present but all are treated as migratory, resident individuals would inflate the estimate of spawners remaining spawners (1- γ'), causing a completely random process to appear Markovian. Nevertheless, because average skipped spawning probability was similar under both datasets, I see no evidence for this latter possibility.

Given sufficient sample size, I found considerable annual variability in skipped spawning probability estimates, highlighting the importance of accounting for temporal variance to gain a better understanding of HBC spawning dynamics. Therefore, when estimating population demographic parameters, it is not only essential to include skipped spawning, but also to allow for annual variation in skipped spawning probabilities. This need for time-dependent modeling reinforces the value of collecting data under the robust design. Because abundance estimates include only those individuals available for detection, it may be necessary to evaluate sampling availability, in this case skipped spawning, to determine what portion of the total population is included in the abundance estimate. If recovery plans are dependent upon reaching a given population threshold, incorrect interpretation of abundance estimates could falsely prevent attainment of recovery goals. Due to overwhelming model support for sex specific parameterization and substantial differences in transition probability estimates, I acknowledge accounting for sex specific heterogeneity is likely essential to the accurate estimation of demographic parameters. However, sex specificity should be further explored because available data was heavily male biased.

In addition, estimates of average annual survival probabilities were nearly equivalent across datasets. In all cases, my survival estimates were reasonably similar to previous work

from the LCRB. Coggins et al. (2006) presented an age-structured open population model based on LCRB humpback chub sampling from 1989 to 2002. They concluded survival varies by age class with estimated annual survival probabilities for 4 year olds of 0.60 up to 0.80 for HBC $\geq$ 11 years. Due to the high number of parameters necessary to fit their models, they were unable to account for the possibility of temporary emigration. Although my study includes all adult HBC (i.e. 4+ years), my estimates are more reflective of Coggins et al.'s survival probabilities for older adults. A possible explanation for this difference is likely due to accounting for a Markovian temporary emigration process (i.e. skipped spawning). Research by Kendall et al. (1997) shows under standard Cormack-Jolly-Seber open population models, which do not account for temporary emigration due to confounding of detection probability and availability, the result is negatively biased survival and detection probability estimates under Markovian temporary emigration, especially at the end of the time series. When employing a Jolly-Seber model, temporary emigration from the study site, in part, appears to be resolved by reducing survival estimates (Zehfuss et al. 1999). Thus, by accounting for Markovian temporary emigration, I reduce the probability of generating biased parameter estimates. An additional explanation for my estimates being more in-line with survival estimates for older adults, is simply due to increased survival probability during my study period. This explanation is probable given increasing abundance estimates in recent years as compared to declines in the 1990s (Coggins et al. 2006; Van Haverbeke et al. 2013).

Although survival estimates were fairly consistent across time, using the 'all adults' dataset, my most parsimonious model includes time varying annual survival probabilities. Nevertheless, my estimate of process variance is low (i.e. $\sigma^2 = 0.005$), indicating survival does not vary considerably over time. All survival probability estimates do not deviate from within

the 95% credible interval bounds of my grand mean estimate except during 2006 and the terminal two years of the study (i.e. 2009 and 2010). During 2009 and 2010, I saw significantly reduced survival probability estimates. In 2006, annual adult survival probability may have truly been reduced, warranting further exploration into the mechanism causing such a substantial decrease. However, I believe the estimated drop in 2009 and 2010 may be an artifact of either individual heterogeneity in detection probabilities or temporary emigration of marked individuals from the study site. Research by Peñaloza et al. (in press) has shown heterogeneity in detection probability as well as temporary emigration can cause negative bias in terminal time specific survival estimates, with the greatest bias introduced due to temporary emigration. Similarly, Langtimm (2009) found when using a closed robust design mark-recapture model to estimate time varying survival and Markovian temporary emigration probabilities, improper constraint of $\gamma_k^{''}$ and γ_k' (i.e. terminal skipped spawning probabilities) resulted in negatively biased terminal survival estimates. They also found the magnitude of the bias increased as S increased and as the difference between γ_{k-1} and $\gamma_k$increased. Because my estimates of $\gamma^{''}$and γ'were time varying, and I implemented similar *a priori* constraints (i.e. $\gamma_{k=}^{''}\gamma_{k-1}^{''}$and $\gamma_{k=}'\gamma_{k-1}'$) to estimate time varying survival probabilities, it is possible this resulted in a negative bias of the two terminal survival probabilities.

From my modeling analysis, I also estimated annual adult HBC abundance in the LCR, which aids in determining fulfillment of population monitoring objectives. However, because sampling occurred solely on their spawning ground and HBC are skipping spawning events, abundance estimates are not reflective of total population abundance but instead spawner abundance. Therefore, when comparing my abundance estimates to those generated by the USFWS, employing a Chapman modified Petersen closed population estimator, I would expect

similar results, as both depict spawner abundance and not total population abundance. However, when comparing my spawner abundance estimates to those generated during the same time period by the USFWS (Van Haverbeke et al. 2013), my estimates were consistently lower, although following the same trends. The consistently higher estimates generated by the USFWS may be attributable to violations of population closure assumptions, because they allowed a greater time period to elapse between initial capture and recapture events. To estimate abundance, the USFWS uses April hoop-net sampling as the first capture period and May hoop-net sampling as the second capture period; therefore, assuming the population is closed to births, deaths, immigrations and emigrations between these sampling periods. However, because this is a period of peak spawning, in which HBC are likely moving into and out of the LCR, it is probable both immigrations and emigrations are occurring during this time. If true, this type of movement would cause abundance estimates generated using a Lincoln-Petersen estimator to be positively biased for either sampling period (Williams et al. 2002). When generating spawner abundance estimates using a closed robust design mark- recapture model, I ensured population closure by defining secondary sampling periods differently, only allowing one to two days to pass between first and second capture events. Therefore, I believe my estimates of spawner abundance are likely more robust.

When evaluating a potential behavior effect in detection probability, using my 'known migrant' dataset, I found evidence for a negative trap response. Avoidance of hoop-nets is reasonable given they are not baited, and the handling and tagging process may condition fish to evade capture. However, when evaluating my 'all adults' and 'known sex' datasets, I did not find evidence for a trap response. Due to sample size limitations under the 'known migrant' dataset, I attribute this discrepancy to spurious results. Additionally, because I pooled over all

subsequent days of sampling for my second detection period, this may have mitigated a trap response. Thus, I believe further evaluation of a trap response is warranted. Concern has been raised as to potential trap shyness in older HBC, because they have been continually exposed to trapping and may have lower detection due to a behavioral response. Therefore, because I did not evaluate a between season trap response (i.e. across annual sampling events), I believe this would be a logical next step.

Generating unbiased demographic parameter estimates was reliant on fulfillment of closed robust design model assumptions, which in part include: no tag loss and no affect on survival due to tagging. PIT tag retention and mortality studies using surrogate species for juvenile HBC, found high survival (i.e. > 98%) and low tag loss (i.e. 3%), 30 days post abdominal tagging (Childs 2002; Ward et al. 2008), indicating there is likely minimal tag loss and negligible effects on HBC survival due to tagging. Because PIT tags are inserted into the abdominal cavity, tags are not discernable to visual predators, likely making a tagged fish no more susceptible to predation by such species. Additionally, swimming studies have shown PIT tagging and handling has little effect on swimming ability (Ward 2003). However, a 2005 study by Paukert et al. evaluating the effects of repeated hoop-netting and handling on bonytail chub (*Gila elegans*), found reduced growth in fish recaptured multiple times as compared to those never recaptured. These findings raise concern that survival and reproductive success may be negatively affected due to reduced growth in fish handled repeatedly, which warrants evaluation.

A thorough assessment of all model assumptions and constraints is essential to understanding the strengths and limitation of my modeling analysis. Goodness of fit tests showed minimal overdispersion in the data, indicating adult HBC are acting independent from one another, thus fulfilling an important model assumption. Concern, however, has been raised

when using robust design models due to the necessary constraint that survival of the unobservable state (i.e. skipped spawner) is equal to survival of the observable state (i.e. spawner). In the LCRB, uncertainty exists regarding fulfillment of this assumption due to differences in habitat usage and energy exertion between spawners and skipped spawners. Although I was unable to evaluate fulfillment of this assumption, this is an important aspect of HBC life history that should be assessed. If however, a substantial difference existed, this difference would likely have been detected in my median c-hat assessment.

My findings reveal, under current environmental conditions, all adult HBC in the LCRB do not spawn annually, but instead need to build up resources prior to spawning in a subsequent year (i.e. Markovian spawning process). I also show skipped spawning probability has been highly dynamic over time, which suggests there is an environmental component influencing reproduction. Not only do my findings improve understanding of HBC reproductive habits, but they also inform availability for detection during annual sampling events used to evaluate HBC demographic parameters. My research further illustrates how violating estimation model assumptions can bias abundance and demographic parameter estimates, and I demonstrate the importance of accounting for such violations. Thus, the results of my study can be used to aid in HBC management and to strengthen insight into the spawning dynamics of this long-lived fish.

Tables

Table 1.1. Effective sample size based on estimation procedures from program MARK for all datasets used to evaluate demographic parameters for the Little Colorado River population of humpback chub from 2001 to 2011.

Dataset	Effective Sample Size
Known Migrant	883
All Adults	9481
Known Sex	3731

Table 1.2. Top robust design mark-recapture models, based on AICc ≤ 7, used for evaluating demographic parameters of the Little Colorado River population of humpback chub. The most parsimonious model is indicated by ΔAICc = 0.0. Three datasets were incorporated to account for potential differences in demographic parameters based on migratory status and sex. $p(t)$ $c(t)$ indicates annual time variation and behavior effect in detection probability. $p(t,j)$ indicates both within and between season variability in detection probability. I evaluated both time constant (.) and time varying (t) survival (S) and skipped spawning probabilities (γ'' (i.e. a spawner transitions to a skipped spawner) and γ' (i.e. a skipped spawner remains a skipped spawner)) and tested three hypotheses for the process driving skipped spawning (i.e. random, Markovian or no skipping).

Dataset	Top Models	ΔAICc	Likelihood	Weight
Known Migrant	**Random - S(.) γ(.) p(t) c(t)**	**0.0000**	**1.0000**	**0.5149**
	Markovian - S(.) γ''(.) γ'(.) p(t) c(t)	1.8163	0.4033	0.2077
	Markovian - S(t) γ''(.) γ'(.) p(t) c(t)	1.9532	0.3766	0.1939
	Random - S(.) γ(t) p(t) c(t)	4.0189	0.1341	0.0690
All Adults	**Markovian - S(t) γ''(t) γ'(t) p(t,j)**	**0.0000**	**1.0000**	**0.5671**
	Markovian - S(.) γ''(t) γ'(t) p(t,j)	1.6601	0.4360	0.2473
	Random - S(t) γ(t) p(t,j)	2.2353	0.3271	0.1855
Known Sex	**Markovian - S(.) γ''(t) γ'(t) p(t,j) - sex variation**	**0.0000**	**1.0000**	**0.6309**
	Random - S(t) γ(.) p(t,j) - sex variation	3.0619	0.2163	0.1365
	Random - S(.) γ(t) p(t,j) - sex variation	3.3099	0.1911	0.1206
	Markovian - S(t) γ''(.) γ'(.) p(t,j) - sex variation	3.5378	0.1705	0.1076

Table 1.3. Parameter estimates from the most parsimonious robust design mark-recapture models under each of the three datasets used to evaluate humpback chub demographic parameters for the Lower Colorado River Basin population. Estimates are from MCMC random effects models. μ indicates the grand mean and σ^2 indicates the associated process variance. If the most parsimonious model included time constant parameterization, I did not include an estimate of process variance, which is indicated by NA*. Estimates are included for survival (*S*) and skipped spawning probabilities (γ'' (i.e. a spawner transitions to a skipped spawner) and γ' (i.e. a skipped spawner remains a skipped spawner)) with sex specific parameterization, if applicable. The grand mean and process variance for female γ' were unknown (i.e. Unk.) owing to parameter estimability issues.

Analysis	$\mu(S)$	$\sigma^2(S)$	$\mu(\gamma'')$	$\sigma^2(\gamma'')$	$\mu(\gamma')$	$\sigma^2(\gamma')$
Known Migrant	0.79	NA*	0.65	NA*	0.65	NA*
All Adults	0.75	0.005	0.45	0.306	0.60	0.085
Known Sex: male	0.78	NA*	0.46	0.277	0.60	0.065
female	0.76	NA*	0.55	0.016	Unk.	Unk.

Figures

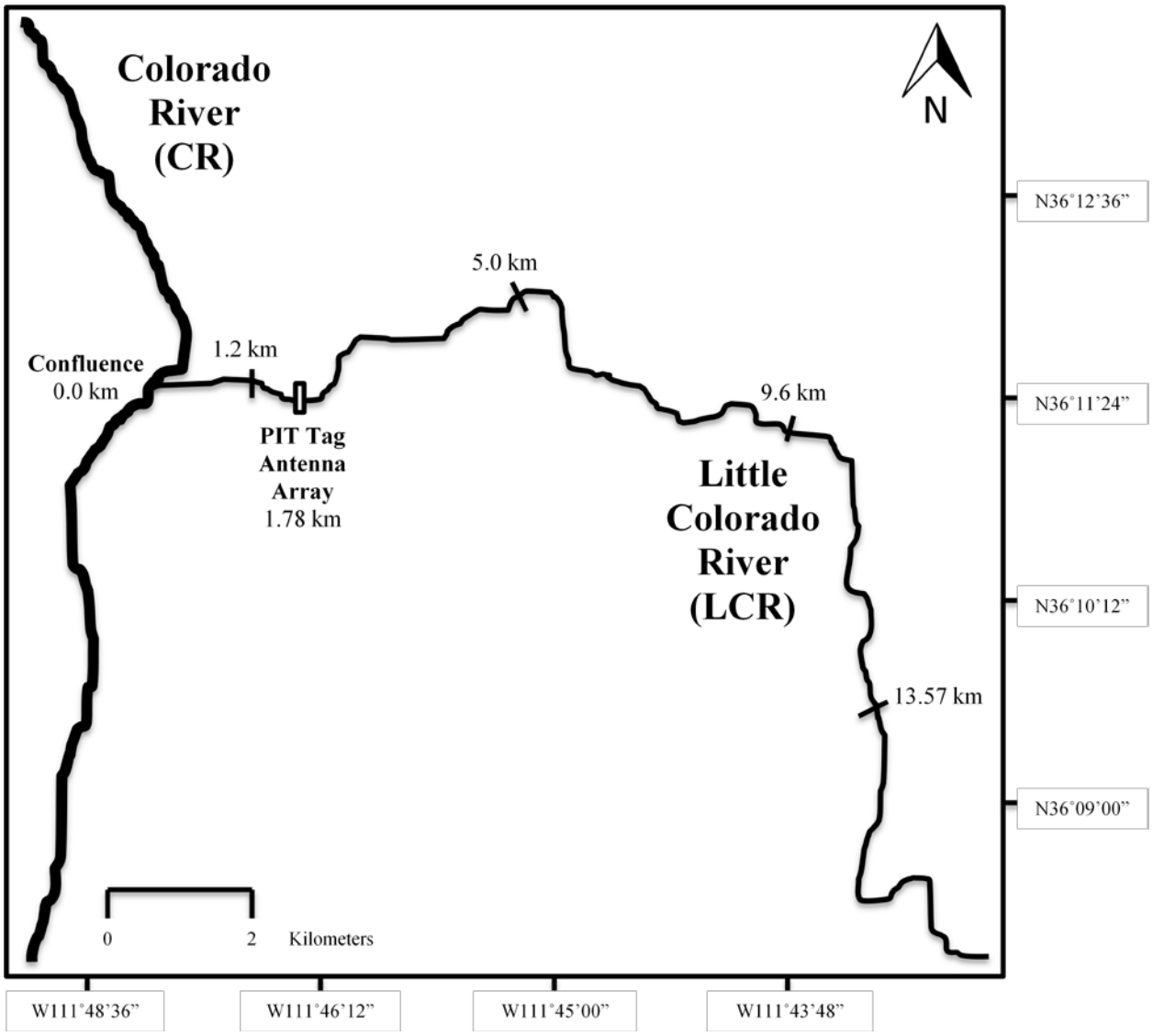

Figure 1.1. U.S. Fish and Wildlife Service (USFWS) primary hoop-net sampling reaches for the federally endangered humpback chub (*Gila cypha*; HBC) in the Little Colorado River (LCR), Arizona as indicated by km markers (i.e. Boulders Reach: 0.0 – 5.0, Coyote Reach: 5.0 – 9.6, Salt Reach: 9.6 – 13.57). Each primary reach has been subdivided into three secondary reaches for a total of nine secondary reaches. Addition hoop-net sampling, conducted by the Arizona Game and Fish Department, occurs from the confluence to km 1.2 in the LCR. Included is the location of the U. S. Geological Survey, Grand Canyon Monitoring Research Center (GCMRC), full duplex PIT tag antenna array showing proximity to the Colorado River (CR).

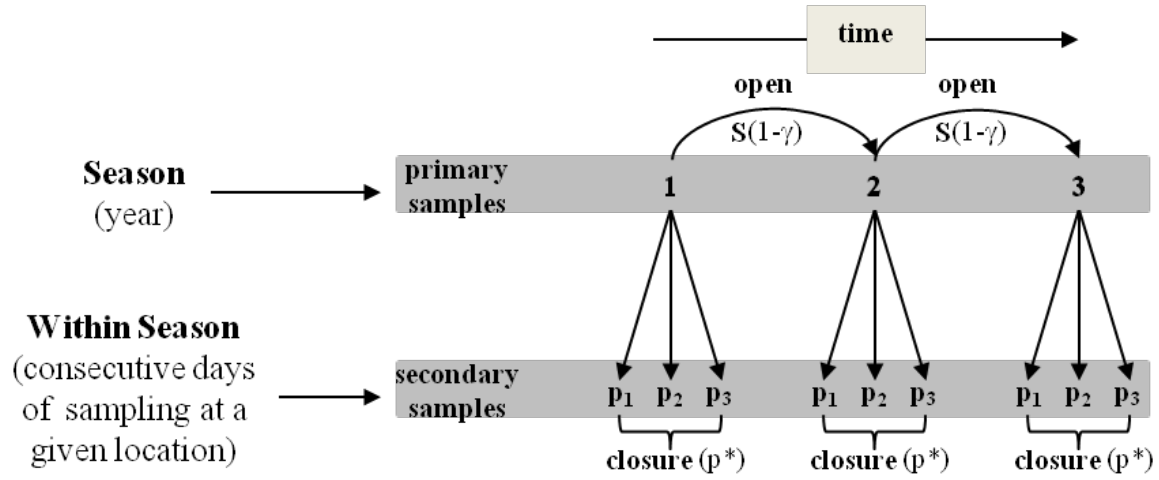

Figure 1.2. Robust design mark-recapture model used to evaluate demographic parameters for the Lower Colorado River Basin population of humpback chub. Data is from U.S. Fish and Wildlife Service hoop-net surveys from the Little Colorado River (LCR), Arizona and LCR PIT tag antenna array detections provided by the U.S. Geological Survey, Grand Canyon Monitoring and Research Center. S = annual survival probability, γ = annual skipped spawning probability, p_1 = hoop-net detection probability - day 1 of sampling at a given location (pooled across April & May), p_2 = hoop-net detection probability - days 2 and 3 of sampling at a given location (pooled across April & May), p_3 = array detection probability - pooled across May, p^* = probability of being detected at least once within a season $[1-(1-p_1)(1-p_2)(1-p_3)]$

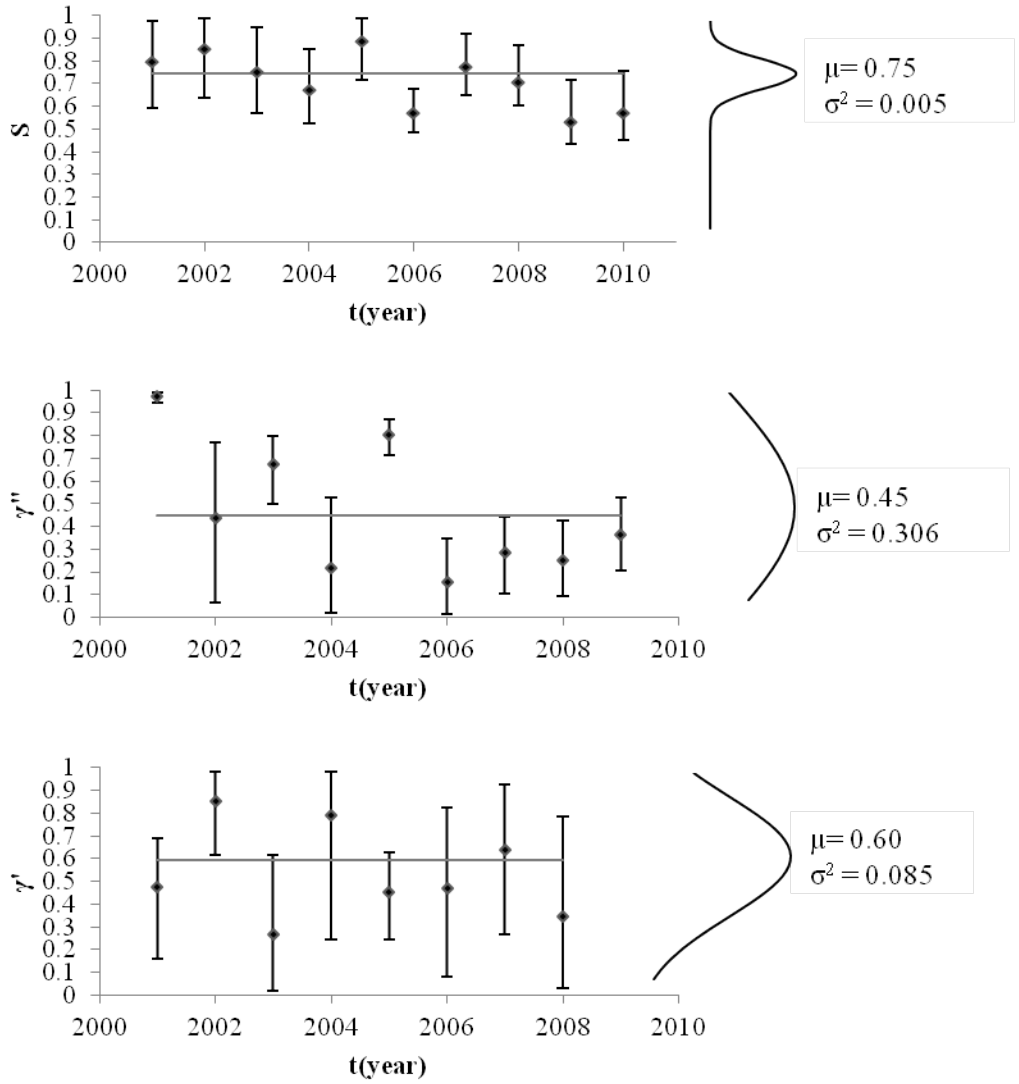

Figure 1.3. Time varying annual survival (S) and skipped spawning probability estimates (γ'' (i.e. a spawner transitions to a skipped spawner) and γ' (i.e. a skipped spawner remains a skipped spawner)) for all adult (i.e. ≥ 200 mm total length) humpback chub in the Lower Colorado River Basin. μ indicates the grand mean over the duration of the study and σ^2 gives the process variance. The distribution on the right illustrates the amount of variability in time varying estimates. Error bars show 95% credible intervals for each estimate.

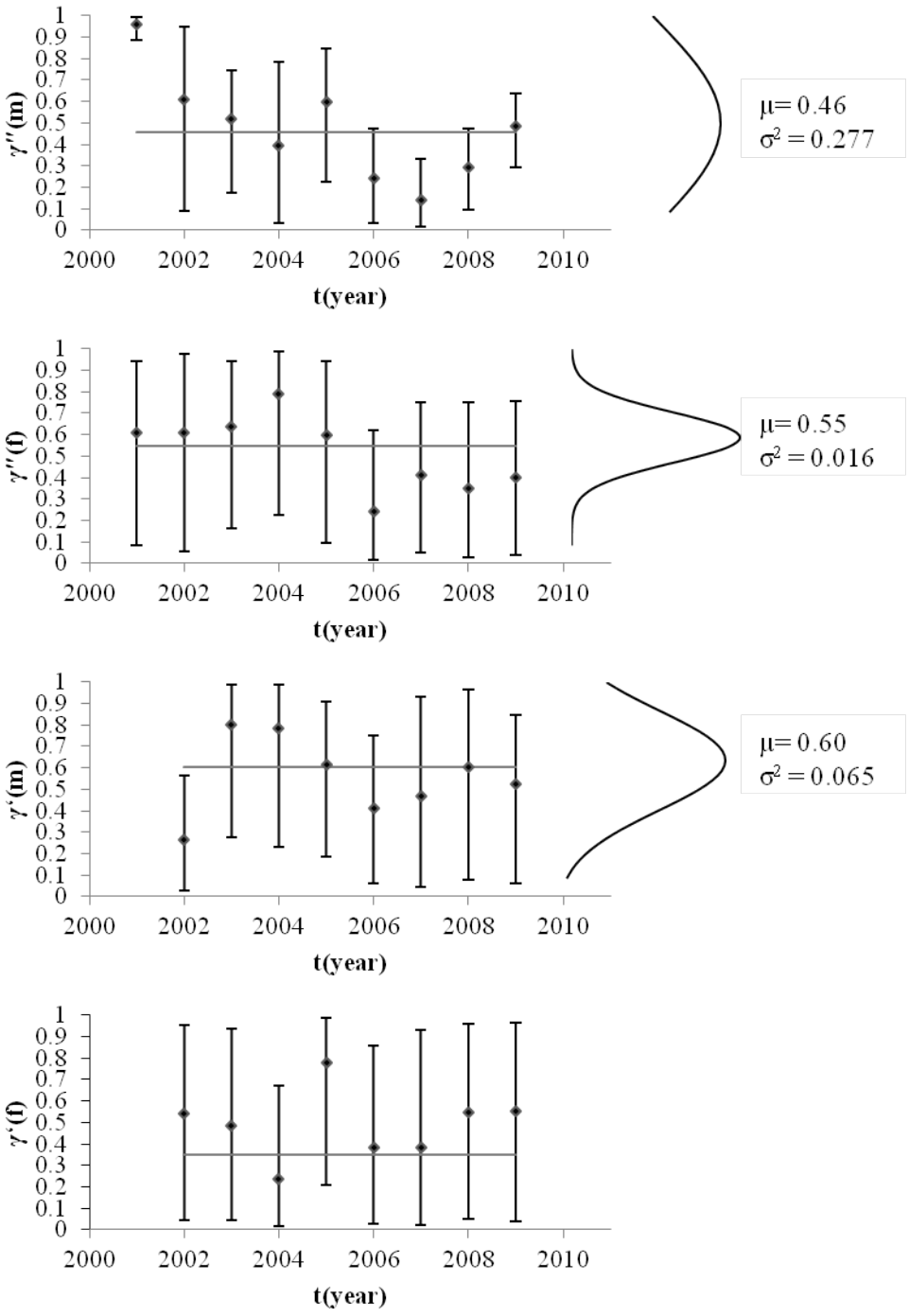

Figure 1.4. Time varying skipped spawning probability (γ'' (i.e. a spawner transitions to a skipped spawner) and γ' (i.e. a skipped spawner remains a skipped spawner)) estimates for 'known sex' adult (i.e. ≥ 200 mm total length, m = male, f = females) humpback chub in the Lower Colorado River Basin. μ indicates the grand mean over the duration of the study, and σ^2 gives the process variance. The distribution on the right illustrates the amount of variability in the time varying estimates. Error bars show the 95% credible intervals for each estimate. Estimates for γ'(f) μ and σ^2 are not reported owing to estimability issues.

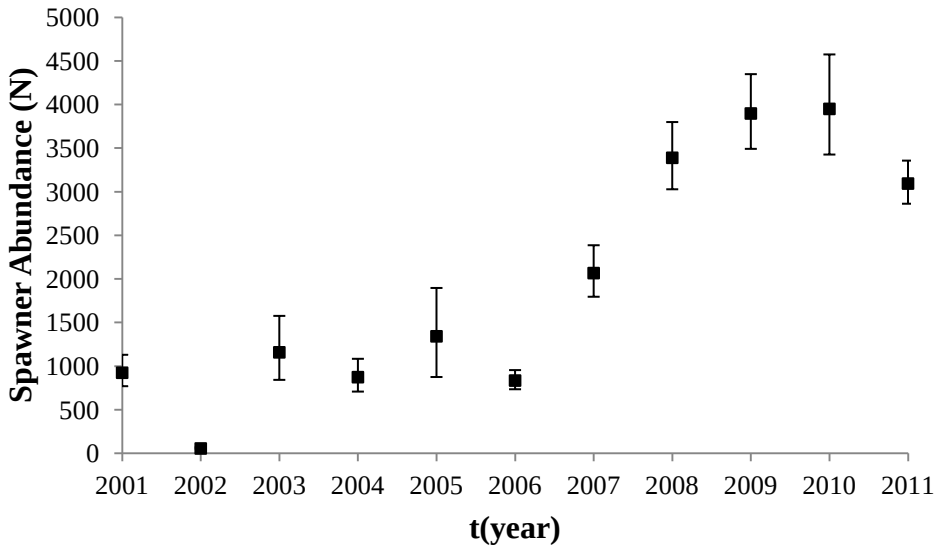

Figure 1.5. Annual spawner abundance estimates for humpback within the Little Colorado River, Arizona with corresponding 95% credible intervals.

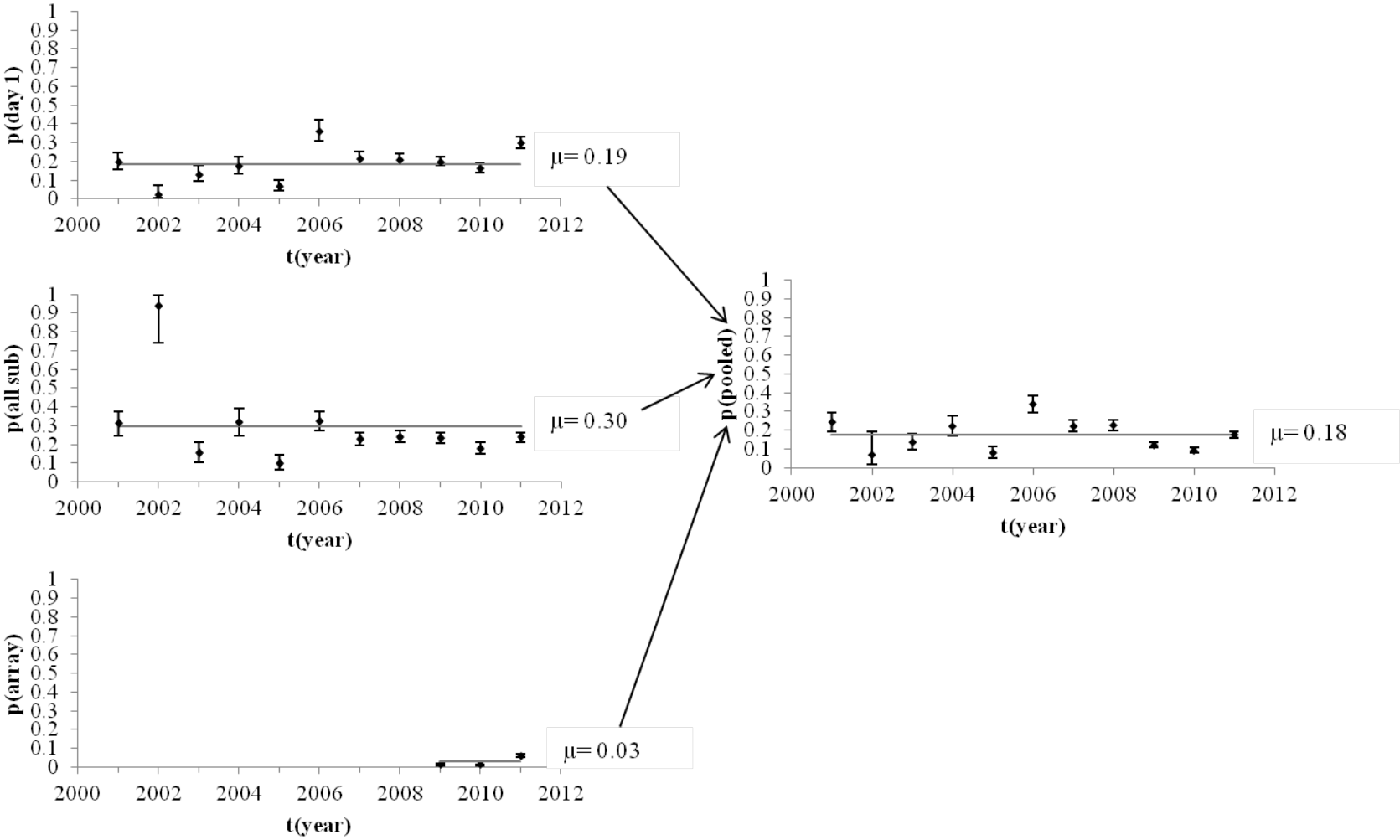

Figure 1.6. Time varying detection probability (*p*) estimates for 'all adult' (i.e. ≥ 200 mm total length) humpback chub in the Lower Colorado River Basin. μ indicates the mean detection probability estimate over the duration of the study. *p*(day 1) indicates day 1 hoop-net sampling detection probability estimates, *p*(all sub) gives detection probability estimates pooled across all subsequent days f sampling at a given locations (i.e. days 2 and 3), *p*(array) is array detection probability estimates pooled across May and *p*(pooled) is pooled detection probability estimates across all within season sampling and gear types (i.e. *p* constant).

CHAPTER 2: SAMPLING METHODOLOGY TRADEOFFS

Introduction

Monitoring sensitive populations is central to informing species recovery. To evaluate population status and trends, monitoring efforts often focus on abundance estimation (USFWS 2002). However, assessment of additional demographic parameters, such as survival and spawning probability, can provide insight into drivers of population change. Generating unbiased demographic estimates presents challenges, primarily due to limited biological understanding, as well as funding, personnel and time constraints. Although, improved parameter estimability may be possible, using technologically advanced and less invasive techniques.

When monitoring sensitive populations, it is ethically and statistically important to minimize human induced negative effects, especially when those effects are a direct result of the monitoring program (Rahel et al. 1999). Handling-induced stress, leading to decreased fitness or mortality, is of utmost concern when population abundance is low. Although handling may not result in direct mortality, stress in fishes has been shown to have cumulative negative effects, including reduced growth and condition (Wedemeyer et al. 1990; Paukert et al. 2001). Research by Paukert et al. (2005) reveals an inverse relationship between growth rate and handling in bonytail chub (*Gila elegans*). Because changes in growth have been found to affect mortality, recruitment dynamics, susceptibility to environmental alterations and trophic interactions (Quist et al. 2012), these findings evoke concern for numerous fish species. For example, fisheries managers are concerned about the potential implications of extensive handling on the federally endangered humpback chub (HBC; *Gila cypha*). Closely related to the bonytail chub, the HBC

is a long-lived species (USOFR 1967; USFWS 2002) experiencing similar handling frequencies (Van Haverbeke et al. 2013). Thus, apprehension has been expressed regarding the current level of handling employed to assess HBC population status and trends in the Lower Colorado River Basin (LCRB). Minimizing human-induced negative effects remains a priority for the LCRB monitoring program, as well as improving understanding of HBC life history strategies and population dynamics (USFWS 2002).

Current monitoring for the LCRB population of HBC has focused on repeated hoop-net sampling within their primary spawning ground, the Little Colorado River (LCR). Due to strong site fidelity (Paukert et al. 2006) and minimal breeding outside the LCR (Valdez and Ryel 1995; Gorman and Stone 1999), it is believed the LCR provides an ideal location for monitoring the entire LCRB population (Paukert et al. 2006). Therefore, the U.S. Fish and Wildlife Service (USFWS), in cooperation with the U.S. Geological Survey, Grand Canyon Monitoring and Research Center (GCMRC), has annually conducted hoop-net sampling in the LCR, to estimate HBC abundance and recruitment (Coggins and Walters 2009; Van Haverbeke et al. 2013). During each sampling event, HBC are evaluated following standard handling procedures, unmarked fish are uniquely marked with Passive Integrated Transponder (PIT) tags, and recaptures are recorded (Persons et al. 2013).

Using a passive detection system for detecting PIT tagged individuals may increase the potential efficacy of monitoring programs. Advantages of supplementing physical recaptures with passive detections include: increased precision of demographic parameter estimates from extra detections and increased understanding of fish dynamics and movement outside of traditional sampling periods. Potential advantages of partially replacing capture effort with

passive detections include: decreasing impacts on fish due to handling and reducing sampling costs while maintaining statistical performance.

To assess the efficacy of passive detection in the LCRB, the GCMRC installed a full duplex PIT tag antenna array (Biomark Inc., Boise, ID), within the LCR, just upstream of the confluence with the Colorado River (CR), to passively detect the passage of tagged fish migrating into and out of the LCR. Placement of the array near the mouth of the confluence suggests the majority of detections will likely consist of migratory HBC, as they move into and out of the LCR to spawn (Douglas and Marsh 1996; Gorman and Stone 1999), and tagged juveniles transitioning to the CR (Limburg et al. 2013). Because the majority of assumed resident HBC are thought to primarily reside in the upper reach of the LCR (Douglas and Marsh 1996; Gorman and Stone 1999; Van Haverbeke et al. 2013), the array was not anticipated to be a reliable method for monitoring resident HBC. However, based on my findings in Chapter 1, as well as work by Yackulic et al. (2014) and Limburg et al. (2013), resident adult HBC (i.e. $\geq$ 200 mm total length (TL)) likely account for only a small portion of the adult population.

Installation of the array afforded an opportunity to assess the effectiveness of using a passive detection system for evaluating HBC demographic parameters. However, tradeoffs in sampling effort may only be possible if demographic parameter estimation is not negatively affected (USFWS 2002). Therefore, I evaluated tradeoffs between hoop-netting and array detections by comparing bias and precision of survival and skipped spawning probability estimates using a simulation analysis that represents the range of scenarios of current interest. I also evaluated the detection potential of the array by empirically estimating detection efficiency. Lastly, I discuss the implications of reduced hoop-net sampling effort on abundance estimation.

Methods

Little Colorado River HBC Monitoring

Repeated hoop-net sampling within the LCR began in the 1980s (Coggins et al. 2006). However, it was not until fall of 2000 that a standard sampling protocol was implemented. Since that time, the USFWS has consistently conducted four annual hoop-net sampling events. Two events occur in the spring (i.e. April and May), to estimate spawner abundance and two in the fall (i.e. September and October), to estimate recruitment. During each sampling trip, three crews are deployed to the lower 13.57 km of the LCR, simultaneously sampling three primary reaches (Salt, Coyote, and Boulders; Figure 1.1). Each primary reach has been divided into three sub-reaches such that the entire lower 13.57 km of the LCR are sampled. Twenty hoop-nets (0.5 – 0.6 m diameter, 1.0 m long, single throat, 3 – 4 hoop, and covered with 6 mm mesh) are deployed in each sub-reach for three consecutive nights. The sampling design results in 180 net nights of sampling effort per primary reach for a total of 540 net nights of sampling effort per event (i.e. 2160 net nights annually). Upon capture, fish are measured, sexed, checked for gametes and parasites, uniquely marked with a 12 mm full duplex PIT tag and released (Van Haverbeke et al. 2013; Biomark Inc., Boise, ID).

The PIT tag antenna array, originally installed in May of 2009, is comprised of multiple individual antennas working in concert with one another (Figure 2.1). The array was designed to cover the full wetted width of the LCR under base flow conditions (~ 220 cfs) and operate year-round. However, spring and summer high flow events, which routinely exceed 2,000 cfs, reduce coverage of the array. Since installation, the array has experienced variable functionality, initially due to an insufficient solar power system used to keep the array functional during winter months as well as high flow events washing out individual antennas. However, the solar power

system was upgraded in 2010 and all damaged arrays have since been replaced. Thus, in recent years, the array has been operational year-round.

Tradeoffs in Sampling Effort

To address possible tradeoffs between hoop-netting effort versus array detections, I considered the following monitoring objectives and practical considerations. First, a priority of the USFWS and GCMRC spring monitoring effort is to assess HBC spawning in the LCR. Second, abundance estimates are key to assessing population status, while survival and skipped spawning probabilities are important for interpreting the causes of population change. However, one question is whether trading hoop-netting effort for array detections negatively affects estimability of abundance, survival or skipped spawning probability.

Reduction in monitoring effort can be achieved by fewer net nights of effort per sampling event, or a reduced number of events. Given the fixed monetary costs of transporting crew and equipment into and out of the study area for a given sampling event, there is a bigger cost savings by reducing the number of events rather than the number of net nights within a sampling event. Therefore, I focused on whether the entire May hoop-netting event could be discontinued.

I chose to evaluate 5 scenarios of spring sampling effort, to assess sampling methodology tradeoffs between hoop-netting and array detections (Table 2.1). My scenarios incorporate variable combinations of hoop-netting and array intensities, and I make comparisons between bias and precision of survival (S) and skipped spawning probabilities (γ'' and γ'). I define γ'' as the probability a spawner in one year skips spawning in the subsequent year, and γ' is the probability a skipped spawner remains a skipped spawner in the subsequent year. Throughout this study, I sought to answer two main questions. First, can May hoop-netting be discontinued and replaced with spring array detections, without negatively affecting demographic estimates?

Second, do array detections contribute additional value to April and May hoop-netting, or should one component be modified or discontinued?

Parameter Values

In part, I obtained parameter values for my simulations from Chapter 1, in which I showed that survival, skipped spawning, and detection probabilities varied annually. I then simulated detection histories based on annual estimates of survival and skipped spawning probabilities (Table 2.2). However, to determine hoop-netting detection probability estimates for April only sampling, I reconstructed my most parsimonious model excluding May detections. From this model, I was also able to estimate HBC spawner abundance based solely on April hoop-net detections. I used the findings from my April only evaluation to assess the potential implications of reduced hoop-net sampling effort on abundance estimation. By employing the time-varying survival and spawning probability estimates presented by Pearson et al., in addition to discrete detection probability estimates, I generated data for each of the 5 unique scenarios of interest. Because the array was not fully operational during the period in which my detection estimates were generated, and the array has been experiencing better functionality in recent years, I selected the highest annual array detection probability estimate (i.e. p(array) = 0.06) to represent low end array detectability (i.e. p(array) low). Thus, the differences between my 5 generating models are due to changes in detection probability.

Empirical Detection Probability Estimation

To thoroughly assess tradeoffs in sampling effort, thus identifying a best case scenario for the array, I conducted a field evaluation of the array to determine its detection potential. I estimated detection efficiency of the array in 2012 and 2013 during the month of May when the LCR was at base flow. From this analysis, I was able to generate a high end detection

probability estimate (i.e. *p*(array) high), which I used in my generating models to better depict the array's range of detectability.

I conducted multiple evaluations to gain a deeper understanding of the array's functionality by decomposing *in situ* detection efficiency (IE) into path efficiency (PE) and antenna efficiency (AE; Zydlewski et al. 2006). Path efficiency is the proportion of the cross-sectional area of the river along the path of the array covered by the read range of the antennas. Antenna efficiency is the proportion of tags detected by the array from all tags passing within the read range of the antenna (i.e. if a tag passes within the detectable range of the antenna, what is the probability it will be detected?). *In situ* efficiency, therefore, is the overall detection efficiency of the array and the product of PE x AE (Zydlewski et al. (2006)). Thus, IE informs the probability a tagged fish crossing the array will pass within its detectable range and be detected.

I evaluated path efficiency by attaching a PIT tag to the end of a meter stick and slowing moving the tag away from the antenna until it was no longer detectable. I measured the maximum detection distance from each antenna by taking multiple measurements over evenly spaced increments (i.e. every 1.5 m). Given the rectangular design of the antennas and their placement within the water column, I took measurements on both the upstream and downstream sides. In certain areas, fish could cross both above and below the antennas, so I measured detection distance from the top and bottom edges for portions of the antennas that were not anchored directly to the bottom of the river. All measurements were taken with the PIT tag oriented perpendicularly to the horizontal plane of the antenna, because this orientation has been shown to provide optimal detectability (Bubb et al. 2002; Hill et al. 2006; Bond et al. 2007). I completed three measurements at each 1.5 m increment for a total of 318 estimates in 2012 and

192 in 2013. The reduction in measurements taken between years is attributable to one of the antennas not functioning in May of 2013. After determining maximum detection distances from the antennas, I then measured the cross-sectional area of the river along the array. Using both measurements, I estimated the proportion of the cross-sectional area along the path of the array in which a tagged fish could be detected when crossing:

$$(\text{PE} = \frac{\text{Area covered by the read range of the array}}{\text{Cross-sectional area of the river along the array}}).$$

To measure AE, I implemented two evaluation techniques. The first focused on tag orientation (AE-Stick) and the second fish behavior (AE-Fish). When evaluating AE-stick, I used a PIT tag attached to the end of a meter stick and passed it within the read range of the antenna at three different orientations (i.e. parallel, perpendicular and 45˚ angle), using the same locations as when measuring path efficiency. I completed a total of two passes for each orientation at each location, yielding a total of 576 passes in 2012 and 646 in 2013. After each pass, I documented whether or not the tag was detected and used this data to determine the proportion of tags detected at each orientation. To better incorporate fish behavior, I employed caged, tagged humpback chub, bluehead suckers (BHS; *Catostomus discobolus*) and flannelmouth suckers (FMS; *Catostomus latipinnis*) to measure antenna efficiency (AE-Fish). A total of 20 fish, ranging in size from 173 to 440 mm TL, were used in 2012 (11 HBC, 5 FMS and 3 BHS), and 30 in 2013 (16 HBC, 8 FMS, and 6 BHS). I supplemented my limited sample of adult HBC with BHS and FMS to increase sample size. I attached an approximately 1.5 m x 1.5 m, mesh bottom, floating PVC cage above a single antenna in the array and marked the top of the detectable range (Figure 2.2). I then released a tagged fish into the cage and allowed it to swim freely for 15 minutes. During this time, I observed when the fish passed within the detectable range and noted whether or not it was detected by the array and calculated:

(AE-Fish = $\frac{\text{\# of detections}}{\text{Total \# of crosses}}$). The same formula was used to calculate AE-Stick for each orientation.

Using my average estimates of PE and AE, I indirectly estimated IE as the product of PE and AE. Due to the rectangular shape of each antenna and the limited read range inside the antennas, a fish has two opportunities to be detected when crossing a single antenna. Therefore, the probability of being detected at least once when crossing within the detectable range of an antenna is [1-(1-p_1)*(1-p_2)], where p_1 is the probability of being detected on the downstream side and p_2 is the probability of being detected on the upstream side. The equation then for overall detection efficiency is: IE = 1-(1-$\widehat{\overline{AE}}$*$\widehat{\overline{PE}}$)^2.

I also estimated IE directly through an intensive hoop-net sampling effort. To do so, I fished 40 unbaited hoop-nets within 500 meters of the array. Twenty nets were placed upstream and twenty downstream. Hoop-nets were fished for 7 consecutive nights, and checked every morning. All captures were measured, sexed, checked for gametes and parasites, scanned for an existing PIT tag, and if the fish was of sufficient size (≥ 100 mm TL) and had not been previously tagged, it was implanted with a 12 mm full duplex PIT tag and released (Biomark Inc., Boise, ID). Any fish, which included HBC, BHS and FMS, captured both upstream and downstream of the array were evaluated to determine if they were detected by the array when crossing (N_{2012} = 37, N_{2013} = 26). In 2012, I also included USFWS hoop-net captures from this area as sampling was concurrent, which increased sample size from 13 to 37. I then directly estimated *in situ* efficiency as: IE = $\frac{\text{\# tagged fish detected by the array}}{\text{\# tagged fish known to have crossed the array}}$.

By using intensive hoop-net sampling to estimate detection efficiency, I was able to better incorporate the path a fish might take when crossing the array and how they are oriented relative to the antenna. Thus, I believe my direct IE estimates likely provide the most reliable

estimates of PIT tag detectability using the array, under base flow conditions. Therefore, I employed these estimates to represent the detection potential of the array when simulating sampling methodology tradeoffs. Because HBC may be crossing the array under higher flows, I believe these estimates likely represent maximum detectability.

Simulations

Although my primary objective was to evaluate tradeoffs in the performance of parameter estimators for my 5 proposed sampling scenarios, I also wanted to assess my ability to detect effects regarding HBC skipped spawning as related to life history strategies. In Chapter 1, I found that HBC in the LCRB skip spawning events, and this process appears to be Markovian. Therefore, I generated data under Markovian skipped spawning probabilities. I then evaluated the power to detect this Markovian process, by analyzing generated data assuming Markovian, completely random, or no skipping strategies (Table 2.3). I completed 500 simulations for each skipped spawning model, for a total of 1500 evaluations per sampling scenario. From these simulation models, I compared bias and precision using April and May hoop-net sampling as a reference condition. I generated average bias estimates for each parameter by determining the absolute difference between its generating parameter value and its estimate. I also computed an average coefficient of variation (CV) for each estimator. I allowed all parameters to vary annually and calculated averages across all 500 simulations for both bias and CV.

All simulations were run in Program MARK (White and Burnham 1999) using a multistate closed robust design model (Kendall et al. 1997). I chose this model because it can account for a reduction in the number of tagged fish due to discontinuing May hoop-netting. I estimated initial spawner population size using average spawner abundance estimates from 2007 to 2011, as I presented in Chapter 1. I then employed annual survival and skipped spawning

probability estimates from Chapter 1 to estimate the number of new recruits needed to maintain stable population abundance for simulation analysis. Thus, I was able to account for both changes in detection probability and number of tagged fish when evaluating these sampling methodology tradeoffs.

Results

Detection Efficiency

In situ detection efficiency of the array was consistent across years, despite variability in the number of functional antennas, with an estimated detectability of 0.42 based on intensive hoop-net sampling (Table 2.4). However, due to a single antenna not being operational in May 2013, I estimated a decrease in path efficiency, leading to a decrease in indirect *in situ* efficiency estimates, while direct estimates remained unchanged. These findings suggest HBC may have been traveling similar paths when crossing the array that excluded the non-functional antenna. Interestingly, average read range from the array increased from 7.5 (95% CI: 7.0, 8.0) cm in 2012 to 15.6 (95% CI: 15.1, 16.1) cm in 2013, when there were fewer operational antennae within the array, potentially indicating a tradeoff in the number of functional antennas in the array and the read range of each antenna. Although I found slight differences in indirect *in situ* efficiency estimates, overall my results were reasonably consistent across years and evaluation methods, with an average detection efficiency estimate of 0.41 (95% CI: 0.38, 0.43).

I found that tag orientation appears to play a significant role in antenna efficiency. When a tag was oriented parallel to the plane of an antenna it was rarely detected (i.e. average 0.02 (95% CI: 0.00, 0.03) across years). However, when oriented at a 45˚ angle, detectability was greatly increased (i.e. average 0.81 (95% CI: 0.77, 0.85) across years) and the highest detectability (i.e. 0.92 (95% CI: 0.89, 0.95)) occurred when the tag was orientated

perpendicularly. Thus, average antenna efficiency, based on tag orientation, was 0.58 (95% CI: 0.55, 0.61), assuming equal probability of each tag orientation, and increased slightly when incorporating fish behavior (i.e. 0.67 (95% CI: 0.63, 0.72) in 2012 to 0.73 (95% CI: 0.68, 0.77) in 2013). This suggests HBC do not cross antennas with equal probability of each orientation.

Simulation: Bias and Precision

When reducing capture effort by replacing May hoop-netting with array detections, I found that bias and precision of demographic parameters (i.e. *S*, γ", γ') were nominally affected. If detection probability on the array was low (i.e. 0.06), minimal bias in survival and skipped spawning probabilities were introduced, 1 – 2% over current hoop-net sampling, and precision was reduced by 2 – 7% (Table 2.5, Figure 2.3). However, when detection probability on the array was high (i.e. 0.42), parameter estimability was actually improved, and in certain cases, considerably (i.e. precision of γ" increased by 15%).

When assessing the value of conducting all three sampling efforts, I found small-sample bias was reduced and precision was increased. On average, bias was decreased by 2% and precision was increased by up to 18%. Even when detection probability on the array was low, I still found a slight improvement over hoop-netting alone (i.e. precision increased by 1% for *S*, 2% for γ′ and 7% for γ"). However, bias was minimally affected (i.e. <1% reduction for S, γ″ and γ′). It is important to note that even under the current best case scenario, which includes all three sampling methods and high detection probability on the array, I still found slight bias in survival and skipped spawning probability estimates (avg. = 2 – 3%; Figure 2.3).

Across all bias and precision comparisons for each of the 5 sampling scenarios, $\hat{S}$ was the least affected by changes in sampling effort, while estimates of skipped spawning probabilities

were most sensitive to changes therein (Figure 2.3). Not surprisingly, I also found that change in precision was more sensitive to sampling methodology tradeoffs than change in bias.

Simulation: Model Selection

I found all simulations resulted in the generating model being most parsimonious, with one exception. When May hoop-netting was replaced with array detections and detection probability on the array was low, 1% of simulations yielded a completely random skipped spawning process as most parsimonious. Overall, evaluations of all 5 sampling scenarios indicated sufficient power to detect the presence of non-annual spawning and under the majority of sampling scenarios, the results correctly indicated the spawning process was Markovian.

Abundance Estimation

Based on hoop-net captures from 2001 to 2011, the discontinuation of May hoop-net sampling resulted in an overall negative bias in HBC spawner abundance in the LCR (Figure 2.4). With the exception of 2006, all other annual abundance estimates are below those presented in Chapter 1 which include both April and May hoop-net sampling periods.

Discussion

Our study reveals that hoop-net sampling within the LCR can be reduced and supplemented with array detections without negatively affecting adult survival and skipped spawning probability estimates, given detection probability of the array reaches its full potential. Alternatively, if array detection efficiency remains low, I expect minimal increase in bias and variability of demographic parameter estimates. Thus, regardless of the detection efficiency of the array, given a minimum detectability of 0.06, parameter estimability should not be substantially affected when replacing May hoop-netting with array detections. However, based on past sampling effort, the discontinuation of May hoop-netting will likely lead to negatively

biased spawner abundance estimates, due to the probable absence of a substantial number of spawners in April, unless ideal timing can be determined when all spawners are present in the LCR. By accounting for a reduction in the number of tagged fish, due to the hypothesized discontinuation of May hoop-netting, my findings provide a robust depiction of potential future monitoring efforts in the LCR.

It is important to note that my evaluation accounts for all spawning HBC having some probability of being detected by the array. If, however, resident individuals are remaining in the upper portions of the LCR and, as a result, never cross the array, resident fish would only be detectable using hoop-net sampling. Thus, when making the decision to discontinue May hoop-netting this factor should be considered.

Given the array has experienced better functionality in recent years, I expect array detection probability will increase over the low estimates I presented in Chapter 1. Instead, array detection probability will likely approach my *in situ* estimate of 0.42, if current functionality is maintained. If array detection probability reaches this level, parameter estimability for survival and skipped spawning probabilities would actually improve over hoop-netting alone. Because the array allows for decreased handling of HBC through replacement of hoop-net sampling, while also improving understanding of HBC dynamics outside traditional sampling periods, I believe the array provides a more effective sampling method over hoop-netting alone, especially given my findings of the array's detection potential.

I acknowledge that in some instances my estimates of the array's detectability may be too conservative and in others too optimistic. First, my *in situ* estimate only accounts for detection on a single array. However, I know that migratory adult HBC will likely cross the array at least twice in any given reproductive year, once when swimming upstream to spawn and second when

migrating back to the CR after breeding (Douglas and Marsh 1996; Gorman and Stone 1999). Therefore, detection by the array will likely exceed my low array detection probability that only accounts for a single detection. Additionally, the installation of a second array in May 2012 should further increase the detection potential of this passive detection system. However, detection by the array could be lower than I expect during in-migration because HBC enter the LCR during the descending limb of the spring hydrograph, when the river exceeds base flow conditions (Gorman and Stone 1999) and it is likely, detection probability is reduced during this time. Although, during out-migration, HBC are likely exiting the LCR during base flow conditions (Gorman and Stone 1999), thus supporting my high *in situ* estimate.

By employing multiple evaluation techniques and decomposing empirical detection efficiency into its component parts (Zydlewski et al. 2006), I was able to gain an in-depth understanding of the detection potential of the array. For a more thorough evaluation, measurements should be taken under multiple flows. However, assessing detection efficiency under higher flows poses many inherent dangers and may not be possible. Although it is reasonable to conclude that detection efficiency decreases under higher flows, tagged fish may travel along consistent paths, remaining close to individual antennas, in which case detection efficiency may be stable.

While bias and precision of survival and skipped spawning probability estimates were not greatly affected when May hoop-netting was replaced with array detections, it is important to note that discontinuing May hoop-netting limits the ability to estimate spawner abundance. Obviously, the array cannot detect unmarked HBC and therefore cannot be used to determine the ratio of marked to unmarked individuals (Seber 1982). Therefore, if May hoop-netting is discontinued, abundance estimates would only be based on April hoop-netting. However, array

detections can be used to augment estimability of other demographic parameters, including survival and skipped spawning probabilities. If all migratory spawners are available for detection during April, then accurate spawner abundance estimates can be generated under this reduction in hoop-net sampling. Research indicates peak spawning occurs in mid-April into early May (Douglas and Marsh 1996; Gorman and Stone 1999), thus it may be possible that all spawners are available during a single detection event. However, from my comparative analysis of annual spawner abundance, I found an overall negative bias in abundance estimates with the exception of 2006, indicating past hoop-net sampling in April was not conducted at a time when all spawning adults were present in the LCR.

Alternatively, reduced sampling effort can be implemented by decreasing the number of days sampled per trip, thus maintaining hoop-net sampling during April and May. One of the benefits of this type of sampling reduction would be reduced bias in N as when compared to eliminating May hoop-netting, although precision would still suffer. However, simply decreasing sampling days would likely not aid budget savings due to high transportation costs.

When determining additional benefits to be gained from continuing all three sampling efforts, I found that bias and precision of S, γ'' and γ' were improved regardless of whether array detections supplemented April and May hoop-netting or replaced a portion. Additionally, using array detections will improve understanding of HBC life history strategies outside traditional sampling periods, as well as evaluating directionality of movement and informing residence time in the LCR.

The installation of a PIT tag antenna array in the LCR allowed me to explore the benefits and potential shorting comings of employing a passive detection system for monitoring HBC demographic parameters. Although important questions remain unanswered, regarding HBC life

history strategies and population dynamics, array detections can be used to help answer many of these questions. Given concern over handling induced stress, I believe the array also provides an opportunity to reduce handling of this imperiled fish. However, due to uncertainty regarding the functionality of the array and a likely negative bias in annual spawner abundance estimates, current effort should focus on using array detections to improve understanding of HBC life history strategies and population dynamics. Thus, information gained from array detections can be used to refine HBC monitoring programs. Nevertheless, my findings reveal substitution of physical capture with a passive detection system provides a viable means for monitoring HBC in the LCR without negatively affecting estimation of adult HBC survival and skipped spawning probabilities. Based on field evaluation, I found detection potential of the array is significantly higher than my original estimates. Although assessments of PIT tag antennas often reveal detection efficiencies approaching 100% (Axel et al. 2005; Aymes and Rives 2009), I found that when compared to hoop-netting, a detection efficiency of only 42% was sufficiently high to improve demographic estimability, especially given average hoop-net detection probabilities were only p(day 1) = 0.19 and p(all sub) = 0.30. With better functionality of the array in recent years, including year-round operation, additional insight can be gained regarding HBC movement outside traditional sampling periods.

Assessment of monitoring strategies for sensitive populations is integral to species recovery. As I have demonstrated, technological advances provided an opportunity to implement an alternative monitoring strategy for HBC in the LCRB, allowing for decreased handling of this endangered fish. In light of widespread use of PIT tag technology for monitoring aquatic species, antenna arrays provide a realistic method for passive detection (Zydlewski et al. 2006). Given the potential implication of handling induced stress on fishes (Paukert et al. 2005; Baker et

al. 2013), I argue that all monitoring programs should evaluate the feasibility of implementing passive detection techniques. As scientists and managers, it is important to mitigate any negative impacts on population persistence especially those resulting from the monitoring program.

Tables

Table 2.1. Sampling scenarios with associated detection probability estimates (p(day 1) = 1st day of hoop-net sampling at a given location, p(all sub) = pooled days 2 and 3 of hoop-net sampling at a given location, p(array) = pooled PIT tag antenna array detections from May) for monitoring humpback chub demographic parameters in the Little Colorado River, Arizona. Estimates were generated using U.S. Fish and Wildlife Service hoop-net sampling data and U.S. Geological Survey, Grand Canyon Monitoring and Research Center PIT tag antenna array detections. Hoop-netting and low array detection probability estimates are based on research from Chapter 1 of this study, while high array estimates were generated by empirical evaluation.

	Detection Probability Estimates		
Sampling Method	p(day1) hoop-netting	p(all sub) hoop-netting	p(array)
April hoop-netting & low array detections	0.10	0.23	0.06
April hoop-netting & high array detections	0.10	0.23	0.42
April & May hoop-netting	0.19	0.30	0.00
April & May hoop-netting w/ low array detections	0.19	0.30	0.06
April & May hoop-netting w/ high array detections	0.19	0.30	0.42

Table 2.2. Humpback chub (HBC) time varying survival and skipped spawning probability estimates based on my findings from Chapter 1 in which I evaluated HBC demographic parameters in the Lower Colorado River Basin. S_t = survival probability, γ''_t = probability of transitioning to the skipped spawning state, γ'_t = probability of remaining in the skipped spawning state

Parameter	Estimate	Parameter	Estimate	Parameter	Estimate
S_1	0.7697	γ''_1	0.9701	γ'_1	0.0000
S_2	0.7817	γ''_2	0.4180	γ'_2	0.5134
S_3	0.7511	γ''_3	0.6738	γ'_3	0.8094
S_4	0.7233	γ''_4	0.1825	γ'_4	0.3783
S_5	0.7835	γ''_5	0.8042	γ'_5	0.7858
S_6	0.6653	γ''_6	0.1398	γ'_6	0.4871
S_7	0.7562	γ''_7	0.2846	γ'_7	0.5309
S_8	0.7404	γ''_8	0.2426	γ'_8	0.6480
S_9	0.6877	γ''_9	0.3713	γ'_9	0.4766
S_{10}	0.7061	γ''_{10}	0.3713	γ'_{10}	0.4766

Table 2.3. Generating and estimation models used in simulation analysis to evaluate tradeoffs in sampling effort for the Lower Colorado River Basin (LCRB) population of humpback chub (HBC). Models are based on my findings from Chapter 1 in which I evaluated HBC demographic parameters in the LCRB. S = survival probability, γ'' = probability of transitioning to the skipped spawning state, γ' = probability of remaining in the skipped spawning state, p = detection probability, t = annual variability, j = within season variability

Generating Model	**Skipped Spawning Process**
$S(t)$, $\gamma''(t)$, $\gamma'(t)$, $p(.,j)$	Markovian (i.e. $\gamma'' \neq \gamma'$)
Estimation Model	**Skipped Spawning Process**
$S(t)$, $\gamma = 0$, $p(t,j)$	No skipped spawning (i.e. $\gamma = 0$)
$S(t)$, $\gamma''(t)$, $\gamma'(t)$, $p(t,j)$	Markovian (i.e. $\gamma'' \neq \gamma'$)
$S(t)$, $\gamma(t)$, $p(t,j)$	Random (i.e. $\gamma'' = \gamma'$)

Table 2.4. Empirical detection efficiency estimates for the full duplex PIT tag antenna array installed in the Little Colorado River, Arizona.

	Year Evaluated	
	2012	2013*
Path Efficiency (PE)	0.40	0.32
Antenna Efficiency (AE)		
Caged Fish	0.67	0.73
Stick: parallel orientation	0.00	0.03
Stick: perpendicular orientation	0.93	0.90
Stick: 45˚ angle	0.81	0.82
***In situ* Efficiency (IE)**		
Direct: intensive hoop-net sampling	0.42	0.42
Indirect: PE x AE fish	0.46	0.41
Indirect: PE x AE stick	0.41	0.32
Average Read Range	7.5 cm	15.6 cm

* An antenna was not functioning during the 2013 evaluation that had been in 2012.

Table 2.5. Change in bias and precision of HBC survival (*S*) and skipped spawning probabilities (γ″ = spawner transitions to a skipped spawner and γ′ = skipped spawner remains a skipped spawner) from simulation analysis evaluating tradeoffs in sampling effort between hoop-netting (A = April, M = May) and PIT tag antenna array detections (low = low array detection probability, high = high array detection probability) for the Lower Colorado River Basin population of humpback chub.

				Simulation Results							
Sampling	Hoop-netting			**Change in BIAS**				**Change in PRECISION**			
Method	April	May	Array	S	γ"	γ'	Direction	S	γ"	γ'	Direction
A+low	yes	no	low	0.012	0.010	0.019	↑ bias	-0.022	-0.057	-0.069	↓ precision
A+high	yes	no	high	-0.013	-0.017	-0.021	↓ bias	0.023	0.149	0.060	↑ precision
A+M*	yes	yes	no	0.000	0.000	0.000	N/A	0.000	0.000	0.000	N/A
A+M+low	yes	yes	low	-0.004	-0.006	-0.009	↓ bias	0.007	0.065	0.021	↑ precision
A+M+high	yes	yes	high	-0.018	-0.021	-0.029	↓ bias	0.031	0.179	0.079	↑ precision

*All bias and precision comparisons use April & May hoop-netting as a reference

Figures

Figure 2.1. Layout of the full duplex PIT tag antenna array installed by the U.S. Geological Survey, Grand Canyon Monitoring and Research Center in the Little Colorado River, Arizona.

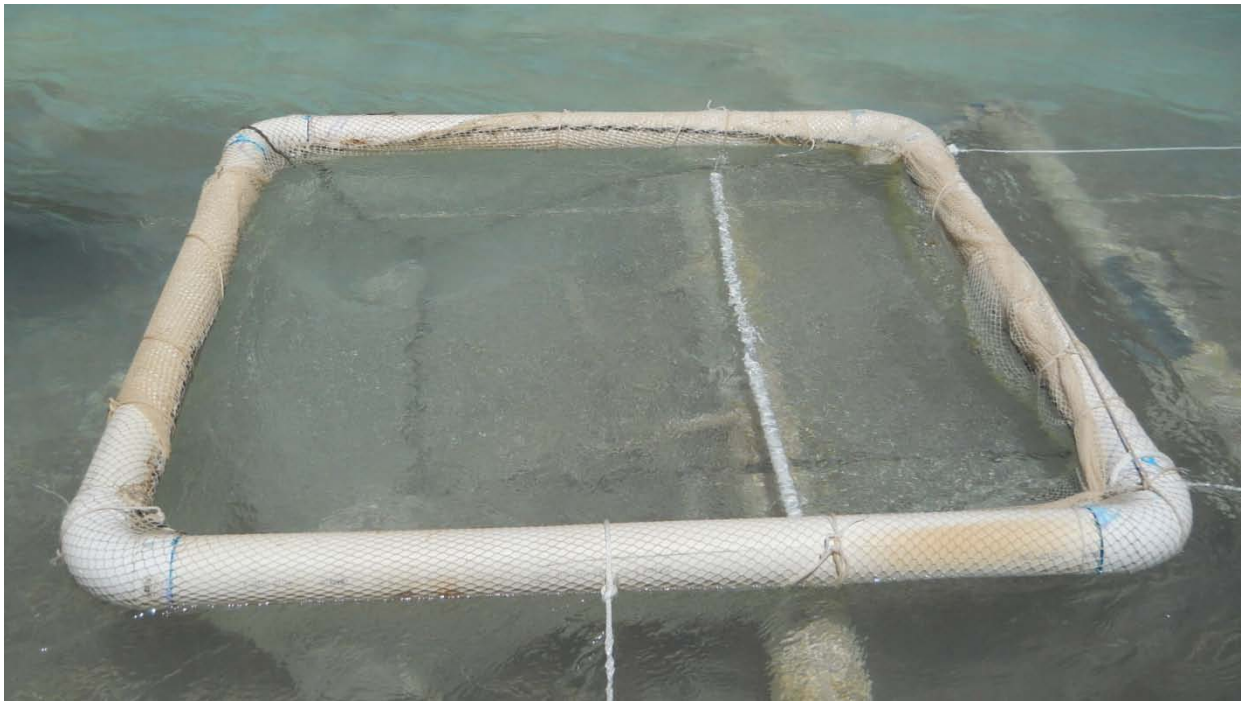

Figure 2.2. Cage used to confine fish for evaluating detection efficiency of the full duplex PIT tag antenna array located in the Little Colorado River, Arizona.

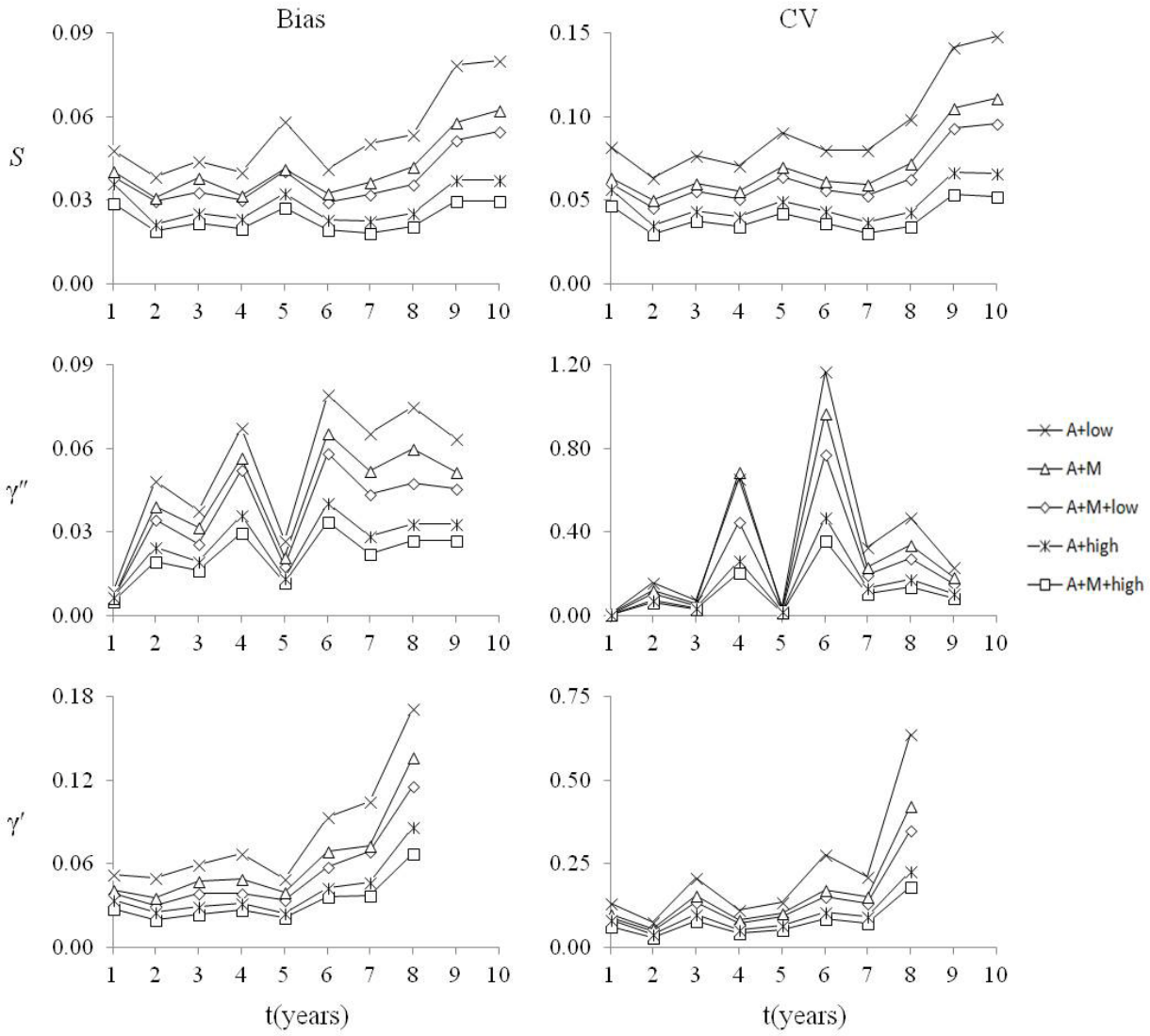

Figure 2.3. Average bias and coefficient of variation (CV) estimates from simulation analysis evaluating sampling methodology tradeoffs between USFWS hoop-net sampling and U.S. Geological Survey Grand Canyon Monitoring and Research Center PIT tag antenna array detections for the Lower Colorado River Basin population of humpback chub. A = April hoop-netting, M = May hoop-netting, low = low array detections, high = high array detections, S = survival probability, γ'' = probability of transitioning to the skipped spawning state, γ' = probability of remaining in the skipped spawning state. Y-axes are not equal across plots.

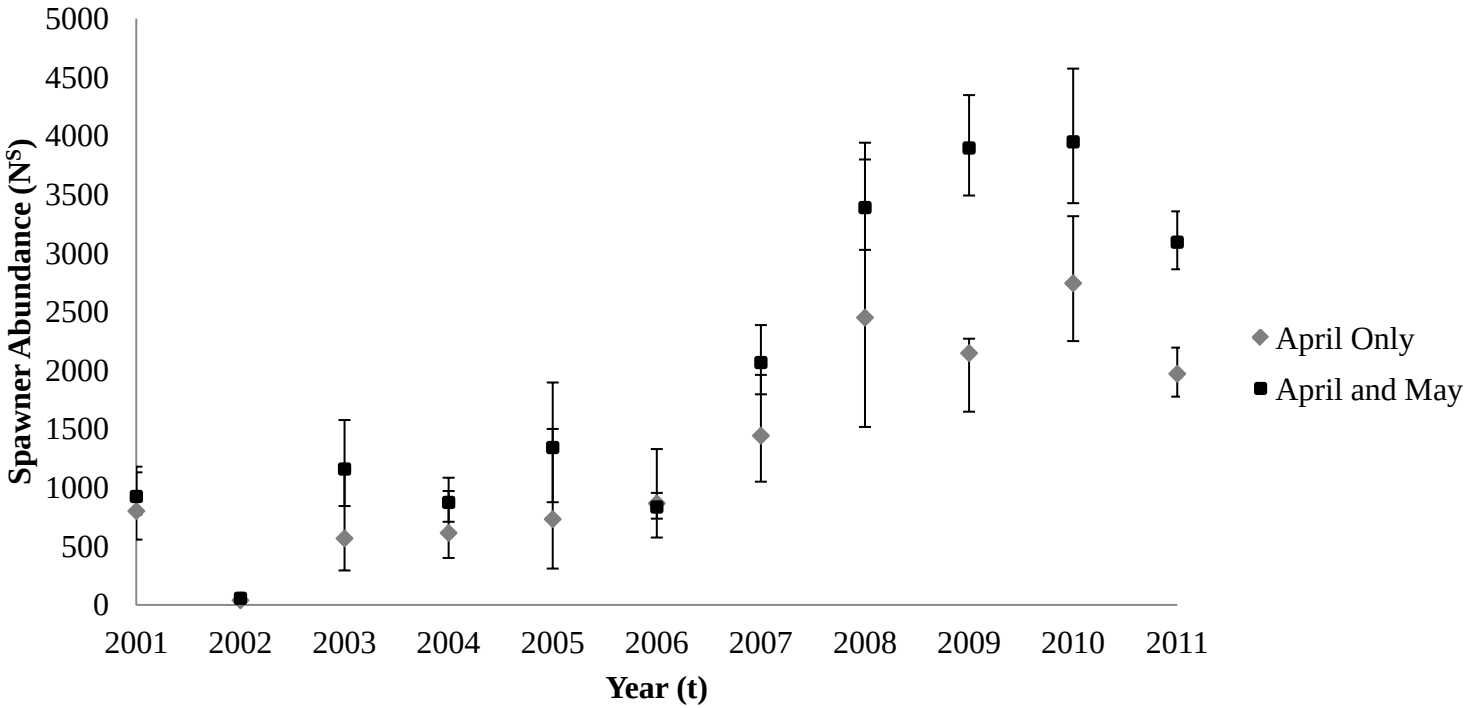

Figure 2.4. Comparison of humpback chub (HBC) spawner abundance estimates with associated 95% credible intervals from the Little Colorado River, Arizona based on varying levels of U.S. Fish and Wildlife Service hoop-net sampling effort. Spawner abundance estimates using hoop-net detections from April and May were presented in Chapter 1.

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APPENDIX: CHAPTER 1 MODEL STRUCTURES

Robust design mark-recapture model structures and number of estimable parameters used to evaluate humpback chub (HBC) skipped spawning (γ), survival (S) and detection (p and c) probabilities along with spawner abundance (N^s), based on detections of adult HBC from 2001 to 2011 in the Little Colorado River, Arizona.

			Number of parameters				
#	Model	Constraints & exceptions	S	γ''	γ'	p	c
1	{Markovian - S(t), γ''(.), γ'(.), p(.), c(.)}	$p_{t3} = c_{t3}$	10	1	1	2	1
2	{Markovian - S(.), γ''(.), γ'(.), p(.), c(.)}	$p_{t3} = c_{t3}$	1	1	1	2	1
3	{Markovian - S(.), γ''(t), γ'(t), p(.), c(.)}	$p_{t3} = c_{t3}$	1	10	9	2	1
4	{Markovian - S(t), γ''(t), γ'(t), p(.), c(.)}	$\gamma_{10} = \gamma_{11}$, $p_{t3} = c_{t3}$	10	9	8	2	1
5	{Markovian - S(t), γ''(.), γ'(.), p(.)}	$p_{t3} = c_{t3}$	10	1	1	2	0
6	{Markovian - S(.), γ''(.), γ'(.), p(.)}	$p_{t3} = c_{t3}$	1	1	1	2	0
7	{Markovian - S(.), γ''(t), γ'(t), p(.)}	$p_{t3} = c_{t3}$	1	10	9	2	0
8	{Markovian - S(t), γ''(t), γ'(t), p(.)}	$\gamma_{10} = \gamma_{11}$, $p_{t3} = c_{t3}$	10	9	8	2	0
9	{Markovian - S(t), γ''(.), γ'(.), p(t,j)}	$p_{t3} = c_{t3}$	10	1	1	25	0
10	{Markovian - S(.), γ''(.), γ'(.), p(t,j)}	$p_{t3} = c_{t3}$	1	1	1	25	0
11	{Markovian - S(.), γ''(t), γ'(t), p(t,j)}	$p_{t3} = c_{t3}$	1	10	9	25	0
12	{Markovian - S(t), γ''(t), γ'(t), p(t)}	$\gamma_{10} = \gamma_{11}$, $p_{t1} = p_{t2}$ & $p_{t3} = c_{t3}$	10	9	8	14	0
13	{Markovian - S(t), γ''(t), γ'(t), p(t,j)}	$\gamma_{10} = \gamma_{11}$, $p_{t3} = c_{t3}$	10	9	8	25	0
14	{Markovian - S(t), γ''(.), γ'(.), p(t)}	$p_{t1} = p_{t2}$ & $p_{t3} = c_{t3}$	10	1	1	14	0
15	{Markovian - S(.), γ''(.), γ'(.), p(t)}	$p_{t1} = p_{t2}$ & $p_{t3} = c_{t3}$	1	1	1	14	0
16	{Markovian - S(.), γ''(t), γ'(t), p(t)}	$p_{t1} = p_{t2}$ & $p_{t3} = c_{t3}$	1	10	9	14	0
17	{Markovian - S(t), γ''(.), γ'(.), p(t,j), c(t)}	$p_{t1} = p_{t2}$ - except t = 9, 10, 11 & $p_{t3} = c_{t3}$	10	1	1	17	11
18	{Markovian - S(.), γ''(.), γ'(.), p(t,j), c(t)}	$p_{t1} = p_{t2}$ - except t = 9, 10, 11 & $p_{t3} = c_{t3}$	1	1	1	17	11
19	{Markovian - S(.), γ''(t), γ'(t), p(t,j), c(t)}	$p_{t1} = p_{t2}$ - except t = 9, 10, 11 & $p_{t3} = c_{t3}$	1	10	9	17	11
20	{Markovian - S(t), γ''(.), γ'(.), p(t), c(t)}	$p_{t1} = p_{t2}$ & $p_{t3} = c_{t3}$	10	1	1	14	11
21	{Markovian - S(.), γ''(.), γ'(.), p(t), c(t)}	$p_{t1} = p_{t2}$ & $p_{t3} = c_{t3}$	1	1	1	14	11
22	{Markovian - S(.), γ''(t), γ'(t), p(t), c(t)}	$p_{t1} = p_{t2}$ & $p_{t3} = c_{t3}$	1	10	9	14	11
23	{Markovian - S(t), γ''(t), γ'(t), p(t,j), c(t)}	$\gamma_{10} = \gamma_{11}$, $p_{t1} = p_{t2}$ - except t = 9, 10, 11 & $p_{t3} = c_{t3}$	10	9	8	17	11
24	{Markovian - S(t), γ''(t), γ'(t), p(t), c(t)}	$\gamma_{10} = \gamma_{11}$, $p_{t1} = p_{t2}$ & $p_{t3} = c_{t3}$	10	9	8	14	11
25	{No Skipping - S(.), γ''(t), γ'(t), p(.), c(.)}	$\gamma = 0$, $p_{t3} = c_{t3}$	1	0	0	2	1
26	{No Skipping - S(t), γ''(t), γ'(t), p(.), c(.)}	$\gamma = 0$, $p_{t3} = c_{t3}$	10	0	0	2	1
27	{No Skipping - S(t), γ''(.), γ'(.), p(.)}	$\gamma = 0$, $p_{t3} = c_{t3}$	10	0	0	2	0
28	{No Skipping - S(.), γ''(.), γ'(.), p(.)}	$\gamma = 0$, $p_{t3} = c_{t3}$	1	0	0	2	0
29	{No Skipping - S(.), γ''(.), γ'(.), p(t)}	$\gamma = 0$, $p_{t1} = p_{t2}$ & $p_{t3} = c_{t3}$	1	0	0	14	0
30	{No Skipping - S(t), γ''(.), γ'(.), p(t)}	$\gamma = 0$, $p_{t1} = p_{t2}$ & $p_{t3} = c_{t3}$	10	0	0	14	0
31	{No Skipping - S(.), γ''(.), γ'(.), p(t,j)}	$\gamma = 0$, $p_{t3} = c_{t3}$	1	0	0	25	0
32	{No Skipping - S(t), γ''(.), γ'(.), p(t,j)}	$\gamma = 0$, $p_{t3} = c_{t3}$	10	0	0	25	0
33	{No Skipping - S(.), γ''(.), γ'(.), p(t,j), c(t)}	$\gamma = 0$, $p_{t1} = p_{t2}$ - except t = 9, 10, 11 & $p_{t3} = c_{t3}$	1	0	0	17	11
34	{No Skipping - S(t), γ''(.), γ'(.), p(t,j), c(t)}	$\gamma = 0$, $p_{t1} = p_{t2}$ - except t = 9, 10, 11 & $p_{t3} = c_{t3}$	10	0	0	17	11
35	{No Skipping - S(.), γ''(.), γ'(.), p(t), c(t)}	$\gamma = 0$, $p_{t1} = p_{t2}$ & $p_{t3} = c_{t3}$	1	0	0	14	11
36	{No Skipping - S(t), γ''(.), γ'(.), p(t), c(t)}	$\gamma = 0$, $p_{t1} = p_{t2}$ & $p_{t3} = c_{t3}$	10	0	0	14	11

Models continued

#	Model	Constraints & exceptions	Number of parameters S	γ''	γ'	p	c
37	{Random - S(t), γ''(.), γ'(.), p(.), c(.)}	$p_{t3} = c_{t3}$	10	1	0	2	1
38	{Random - S(.), γ''(.), γ'(.), p(.), c(.)}	$p_{t3} = c_{t3}$	1	1	0	2	1
39	{Random - S(.), γ''(t), γ'(t), p(.), c(.)}	$p_{t3} = c_{t3}$	1	10	0	2	1
40	{Random - S(t), γ''(t), γ'(t), p(.), c(.)}	$\gamma_{10} = \gamma_{11}$, $p_{t3} = c_{t3}$	10	9	0	2	1
41	{Random - S(t), γ''(.), γ'(.), p(.)}	$p_{t3} = c_{t3}$	10	1	0	2	0
42	{Random - S(.), γ''(.), γ'(.), p(.)}	$p_{t3} = c_{t3}$	1	1	0	2	0
43	{Random - S(.), γ''(t), γ'(t), p(.)}	$p_{t3} = c_{t3}$	1	10	0	2	0
44	{Random - S(t), γ''(t), γ'(t), p(.)}	$\gamma_{10} = \gamma_{11}$, $p_{t3} = c_{t3}$	10	9	0	2	0
45	{Random - S(t), γ''(.), γ'(.), p(t,j)}	$p_{t3} = c_{t3}$	10	1	0	25	0
46	{Random - S(.), γ''(.), γ'(.), p(t,j)}	$p_{t3} = c_{t3}$	1	1	0	25	0
47	{Random - S(.), γ''(t), γ'(t), p(t,j)}	$p_{t3} = c_{t3}$	1	10	0	25	0
48	{Random - S(t), γ''(t), γ'(t), p(t)}	$\gamma_{10} = \gamma_{11}$, $p_{t1} = p_{t2}$ & $p_{t3} = c_{t3}$	10	9	0	14	0
49	{Random - S(t), γ''(t), γ'(t), p(t,j)}	$\gamma_{10} = \gamma_{11}$, $p_{t3} = c_{t3}$	10	9	0	25	0
50	{Random - S(t), γ''(.), γ'(.), p(t)}	$p_{t1} = p_{t2}$ & $p_{t3} = c_{t3}$	10	1	0	14	0
51	{Random - S(.), γ''(.), γ'(.), p(t)}	$p_{t1} = p_{t2}$ & $p_{t3} = c_{t3}$	1	1	0	14	0
52	{Random - S(.), γ''(t), γ'(t), p(t)}	$p_{t1} = p_{t2}$ & $p_{t3} = c_{t3}$	1	10	0	14	0
53	{Random - S(t), γ''(.), γ'(.), p(t,j), c(t)}	$p_{t1} = p_{t2}$ - except t = 9, 10, 11 & $p_{t3} = c_{t3}$	10	1	0	17	11
54	{Random - S(.), γ''(.), γ'(.), p(t,j), c(t)}	$p_{t1} = p_{t2}$ - except t = 9, 10, 11 & $p_{t3} = c_{t3}$	1	1	0	17	11
55	{Random - S(.), γ''(t), γ'(t), p(t,j), c(t)}	$p_{t1} = p_{t2}$ - except t = 9, 10, 11 & $p_{t3} = c_{t3}$	1	10	0	17	11
56	{Random - S(t), γ''(.), γ'(.), p(t), c(t)}	$p_{t1} = p_{t2}$ & $p_{t3} = c_{t3}$	10	1	0	14	11
57	{Random - S(.), γ''(.), γ'(.), p(t), c(t)}	$p_{t1} = p_{t2}$ & $p_{t3} = c_{t3}$	1	1	0	14	11
58	{Random - S(.), γ''(t), γ'(t), p(t), c(t)}	$p_{t1} = p_{t2}$ & $p_{t3} = c_{t3}$	1	10	0	14	11
59	{Random - S(t), γ''(t), γ'(t), p(t,j), c(t)}	$\gamma_{10} = \gamma_{11}$, $p_{t1} = p_{t2}$ - except t = 9, 10, 11 & $p_{t3} = c_{t3}$	10	9	0	17	11
60	{Random - S(t), γ''(t), γ'(t), p(t), c(t)}	$\gamma_{10} = \gamma_{11}$, $p_{t1} = p_{t2}$ & $p_{t3} = c_{t3}$	10	9	0	14	11